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BECOMING HUMAN: HOW EVOLUTION MADE US

Greg Downey

Becoming Human:

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Acknowledgments

Becoming Human started off as a kind of dare.

Well, more than one dare.

In a conference on the future of teaching, I dared my employer, Macquarie University, to embrace open education more fully. I warned that open exchange of teaching materials and online learning was inevitable.

My Associate Dean for Learning and Teaching, Prof. Sherman Young, and Macquarie University's Provost, Prof. Judyth Sachs, dared me to back up my high-sounding call through our partnership with Open Universities Australia. In April, 2013, we launched Macquarie University's first 'MOOC', a 'massive online open classroom.'

This book was prepared to give the students an opportunity to read more closely and to find additional resources and links on the topics covered in that course, 'Becoming Human: Anthropology.'

I have to thank those who have helped at every step. Robert Parker, at Macquarie University, for pitching in all over the place, from conceptualising the course to struggling to reduce thirteen-weeks-worth of material down to six — and then to four — to helping with the creation of the simulator and managing shooting in Melbourne

In Melbourne, Greg Bird did a masterful job, with tight time constraints, of tracking down an immense variety of images to illustrate the lecture-videos and for this book. You can see his work on many pages. He also gave some great feedback on educational design issues.

Thanks to everyone at Macquarie University who made this possible, especially Sherman Young and Judyth Sachs.

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A special debt of gratitude to my wife, Tonia Gray, and my daughter, Mikhaela.

Preface

When colleagues find out I teach human evolution at Macquarie University and Open Universities Australia, they often ask me, 'Why?' Sure, it's a fascinating topic, but it's one that I was not trained to teach.

Like many anthropology students in the United States, I took archaeology classes and studied human evolution when I was doing my bachelor's degree. Two of the many standout classes that I took at the University of Virginia were 'Human Origins' by Jeffrey Hantman and an intense seminar on Mayan archaeology.

But I was trained as a cultural anthropologist in graduate school, prepared to make sense of living people's cultures, to pick up new languages, to live with a group who has a very different way of understanding the world and — over time — make sense of their perspective. In some places, committing to a career in cultural anthropology can mean putting aside evolutionary research and theory because they can often seem only distant causes of contemporary social life. Teaching human evolution, about bones and biology, brains and genitalia, would seem to be a stretch, even for someone who didn't know the field.

To someone who does know anthropology, to my fellow anthropologists, the jump from cultural to biological anthropology can seem even greater. When I took my PhD back at the very end of the 1990s, biological and cultural anthropologists were often convinced that their greatest adversaries were in the other camp: cultural theorists had to argue that culture overcame or transcended biology, biological researchers that culture was just a superficial veneer on a universal biological reality. From this point of view, for a cultural anthropologist to teach human evolution was a bit of betrayal. 'Do you talk about genetics?' some of my cultural colleagues would ask.

Fortunately, that tension has changed.

In the past decade or two, integrative approaches that bring together evolution and social causes, nature and nurture, are in ascendance as the research problems we face — illness, cognitive abilities, differences between men and women — make a mockery of trying to divide up the facets of what make us human.

I'm not alone in trying to bridge the gap these days between biological and cultural approaches to the study of human nature. Anthropologists these days realize that we are not really arguing most with each other: we are arguing primarily with people who pay no attention to human diversity, with commentators who refuse to recognize the importance of evolution, with overly simple explanations for human institutions that we know to be complicated.

But most importantly, anthropologists are arguing with people who think they know how evolution works or think they know about 'human nature,' but don't really have a grasp of the fascinating research results that our field has found over more than a century.

Often, I will read an article in the popular press where a science writer has been talking to some other researcher who thinks he or she knows about human evolution or human diversity (but really mostly does work in a laboratory or by surveying university students). And the article will make proclamations about 'our species, throughout its history,' or 'Humans are all this way because evolution makes us this way,' and I know that the evidence — the hard, cold bones in the ground, or the abundant ethnographic record that comes from studying peoples all over the planet — doesn't support what they're saying.

So that's why I teach human evolution, and why I've written this book. To me, you simply cannot understand how humans are today, right now, all around us, if you do not understand evolution.

However, if you understand evolution badly (including listening to what some quite famous commentators say about it), a little knowledge can be almost as misleading as none at all. And what I read in the newspapers makes me feel like a lot of people out there who think they understand evolution have just a little bit of knowledge and don't even realize it. The closer you get to the scientists, the more interesting the research is, and the less it boils down to a simple story.

The point is not that 'everything is complicated' or that a particular scientist or evolutionary theorist is 'dead wrong.' Often, partial truths can become serious distortions if over-applied; theories that are enormously helpful in clarifying how we see the world can become constraints on our ability to see all the evidence if we cling to them too tightly, as if they are sacred texts. Biology is endlessly surprising; that's one of the great joys of studying evolution.

But human are even more surprising than most species. Human evolution is a very special case, even if we share so much of our DNA with the other living things on the planet.

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To make a long story short, I teach human evolution because, without it, we simply cannot understand ourselves. But if we understand evolution badly, or we cling to a particular theory even in the face of its exceptions, a little evolutionary thinking can also be a problem. I needed an introduction to human evolution that prepared people for the full breadth of anthropology, biological and cultural, archaeological and linguistic.

This electronic book is an attempt to provide a very basic knowledge of human evolution that doesn't teach an overly simple version of evolutionary theory. Because I'm a cultural anthropologist, I'm interested in how our evolutionary legacy continues to affect us to the present day, including how it makes possible all of the technological achievements, social complexity, and cultural variety around the planet.

If we understand evolution, we also understand two very important facts: first, that evolution is certainly not 'over' or finished with us. Second, we have the power to affect our own, and other species', evolution. What we do can change the forces of natural selection, although this may seem counter-intuitive.

In fact, we're not the first species to have this power. We're only alive because other generations of life, long before our ancestors arose, changed the very nature of the planet. But we're doing it now, more than the general public probably realizes, and we need to be aware of this as we make important political, economic, and technological choices going forward.

I'm not just talking about the temperature of the planet or the range of species with which our descendants will share our planet — although both of these are important. One lesson of evolution is that life changes. Recognising how we are participating in that change, and may be affected by it in the future, is one of the great challenges of contemporary anthropology, in cooperation with a lot of other researchers.

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Traces

One reason that we study human evolution is that the origin of our species is relevant to the way we are today. We can see the effects of evolution in our bodies, brains, behaviours, and so much else about us. But we are also left with some pretty challenging questions, especially as biological research shows us the deep links connecting all life: How did humans get to be so unusual?

We're 1-in-450-million

There are at least 9 million species alive on the planet Earth today. Some scientists say this estimate is too low; they say the real number may be as high as 30 million species.

But this 9 or 30 million represents only a *tiny* fraction of all the species that have ever lived. Some scientists argue that *over 98% of all the species that have ever lived are now extinct.* Not just the dinosaurs, but countless, innumerable other species, some of them killed off in five massive extinctions in the history of our planet. In the worst of them, the Permian-Triassic extinction about 250 million years ago, over 90% of all marine species died — even insect species were decimated — and it took the variety of life 10 million years to bounce back.

So conservatively, and I mean very conservatively, there's been at least 450 million different species, most of which are now extinct. All that variety. All these amazing traits, from frill-necked lizards and towering sequoias and narwhals to penguins and armadillos and giant colonies of fungi.

Animals that can live in the most hostile environments, such as bacteria that live by oxidizing iron at the bottom of the sea; xerophyte plants that survive in deserts; microbes that can live in deep salty basins in the Mediterranean, others that thrive in the hot springs at Yellowstone National Park or deep under Antarctic ice. Life deep underground and in the ocean, even inside other life. Creatures that blow our minds with their amazing ability to survive and adapt, proving that evolution will find a way, even in conditions that we think might make life impossible. Enough strange creatures and exotic species for a lifetime of great nature documentaries.

And yet, in a very important way, we're all alone. Humans are a one-in-a-half-billion experiment. Conservatively.

You would get better odds playing Powerball or winning the lottery. No other species has manufactured complex tools, built cities, gone to the moon, written novels, composed symphonies, or produced Lady Gaga. Of all the 450 million or more species, potentially many times more, we seem to be one of a kind. Utterly unique... well, on our planet at least.

This is the central mystery of human evolution: how did evolutionary forces, forces that equally affect the millions upon millions of other species, produce such a strange, balding ape with such peculiar social habits and extraordinarily odd cognitive abilities?

How did evolution produce us from a set of biological building blocks that we increasingly realize we share with other living things? We share a huge proportion of our DNA with chimpanzees, our nearest cousins, for example — some put the number at over 98%. We share a striking proportion of DNA, however, with every living thing. As anthropologist Jonathan Marks put it, we aren't just 98% chimpanzee, we're 30% daffodil or banana.

If we look at the cells of living things, the similarities are obvious, even between plants and animals. The chemicals that make up DNA, the four base codes, are shared; the same four bases combined over and over again in distinct ways to make all life that we know. Evolution wrote the book of life with a remarkably small set of letters.

And yet, that difference, that 2% between us and chimpanzees, for example, is obviously a giant gulf. What makes the gap so great?

Sure, it's a narcissistic question. Yes, there are 9 or 30 million living species out there, millions upon millions that have ever lived, but let's talk about us. Yeah, we're fascinating, especially to us. Well, and to our dogs, too, I suppose, ... although probably not for the same reasons.

It's not just that evolution produced us. Evolution produced an animal capable of understanding evolution. That's extraordinary. A biological process, billions of years old, somehow produced a creature with such extravagant cognitive and social abilities that, working together over about the last 200,000 years or more, we've figured out where we come from.

That's what we'll be exploring over the course of this book: how does evolution work? How does variation arise? Why, of all the orders of life, did primates produce us? When did apes start to look like us, to walk on two feet, and why? How did our ancestors reproduce, and why do we have such helpless babies, so fragile and needing attention? And finally, what's the story of these big, versatile brains that we possess, that allow us to do so much? And what's the price of these big brains, a price many of us may not even realize we're paying?

This book is about our origins. How did we get here?

Although this book will link to documentaries and websites, however, the materials are part of a bigger project. This resource was created for an 'open classroom', which means that we hope to provide you with a chance to talk with other people who are interested in the same subject, to trade ideas, resources, advice, and to learn more together. This book will present things quickly, as do the lecture videos that you can find at Open2Study, but there's lots of space to go deeper into the issues or changes that you find most fascinating. I hope to use this book to provide you with some great places to explore further.

Introducing Anthropology

This course (and the accompanying book) is an experiment for us, both in the Department of Anthropology at Macquarie University and at Open Universities Australia — we've never thrown open our doors quite like this, to anyone, anywhere. We're trying all new sorts of technology and approaches to what we're doing. We wanted to choose a topic that is, at the same time, really exciting, with lots of new research and science, but also philosophically deep and socially important, asking questions that go to the core of who we are and what matters to us. We hope you'll enjoy it and that you'll really join in and enrich the discussion. One thing I know from teaching human evolution to thousands of students is that all kinds of people are fascinated by, well, humans. Our story. It may be controversial, but I'll do my best to share how I think, and I really hope that you'll contribute as well.

I'll be your instructor, in part, although you'll also learn a lot, maybe more, from each other. I'm Greg Downey, an anthropologist trained in the United States, but who moved to Australia in 2005 because I married an Australian.

When I started out as an anthropologist, I didn't study or write about evolution. I went to Brazil to study capoeira, an Afro-Brazilian martial art. Capoeira is a demanding, acrobatic martial art that combines elements of dance and fight. It's really hard and takes years to learn; all the training changes the people who do it. Capoeira practitioners build muscles, become faster and more flexible. They even perceive, move, and react differently — like a lot of martial arts and sports and practices like yoga.

I worked for years on capoeira and wrote a book about it, moved on to study 'cage fighting' or 'mixed martial arts,' and have recently been working on a range of subjects including rugby.

The more I studied sports and how people learned skills, the more I realized that I was studying perhaps the most important thing that makes humans different from other species: we come into the world incomplete. Our bodies and brains can be trained to do an incredibly wide range of things. And we change ourselves, forcing our bodies and brains to adapt to everything from language and education to music, the internet, our hobbies, along the way learning from each other and accumulating generations upon generations of knowledge.

So a few years ago, I began to do neuroanthropology, to study the relationship between brain and culture. Neuroanthropology includes how our brains produce culture, but also how our cultures shape our nervous systems. For example, being born into a community with language means that parts of our brains and ears get shaped by that language. By the time you're a year old, your hearing can pick out speech sounds in your native language, and starts to lose the ability to make fine distinctions important in other languages. To learn to write, or balance on your head, or chase down your dinner on the savannah or use a use a laptop computer means gearing up your body and brain for these purposes.

At the same time, all these activities leave their traces on your body and brain. The illnesses we get, our aches and pains, our senses — they all wind up being shaped by patterns of activity.

The only way to understand this human process, the way we shape ourselves, in my opinion, is to combine the study of culture and biology. We have to recognize that evolution had made us with enormous potential but leaves a lot of the finishing off to our complicated social and symbolic life. Evolution had made us biologically susceptible to culture, just as it had made us capable of producing culture. We are the unfinished ape, the self-made species.

Figuring out how that works, how evolution made us, in my opinion, requires an anthropological perspective. Anthropologists are famous for three things in particular:

First, we study people in the field, where they live, or have lived, not in laboratories. Anthropologists are good at messy, good at digging, good at hanging out and observing what people do. We go to where people (or other primates) are, even if that requires a plane, train and boat, even if that means learning difficult languages or exposes us to nasty sicknesses. How are you going to study the ways humans evolved if you aren't ready to chase them to the four corners of the earth?

Second, anthropologists study human diversity. We don't sit at home or in a café and write deep thoughts about human nature — well, sometimes we do that, I suppose — and we don't just study people like ourselves. We may start by studying a specific group, a tribe, a community, or particular ways of life, sites where our ancestors have left remains. We cast the net as wide as possible and explore the full range of the human condition.

And finally, anthropologists don't respect intellectual borders. Just as I had to start studying biology to understand what I was learning from capoeira practitioners in Brazil, teaching myself neurology and exercise physiology and a whole range of other things, anthropologists believe that you have to look at all the data, even if it stretches your brain to the breaking point. We call this a 'holistic' approach. To study human evolution means looking, not just at human skulls and bones and brains and DNA, but also at other primates, at early tools, at languages, at child rearing, at human sexual variety.

So welcome aboard, and strap in. One thing you'll learn, I hope, is that we don't yet have the final word. New findings might still turn some of the things we thought we knew upside down; I can't use all my slides from five years ago because we know more than we did then.

But the evidence we have is making the story we can tell about our origin more and more complete. I welcome you to bring to the discussions even perspectives that I don't endorse 100% because it's only by having a rollicking, open debate, by putting all the evidence we have on the table, that we're going to get a better and better understanding of what it means to be human, and how we got here.

Evolution isn't over. We're still becoming human. And arguing about how we got here, and what the implications are, is part of this process.

When you had a tail...

Once upon a time, you had a tail.

I'm not singling you out. We all did.

It's nothing to be embarrassed about.

First off, we still have a tailbone, a set of fused vertebrae called the coccyx. If you've hit it hard, such as slipping on ice or falling on your bum, you know what I'm talking about. At the very bottom of our spines, in the middle of our pelvis, there are these vertebrae that are fused together into one triangular lump.

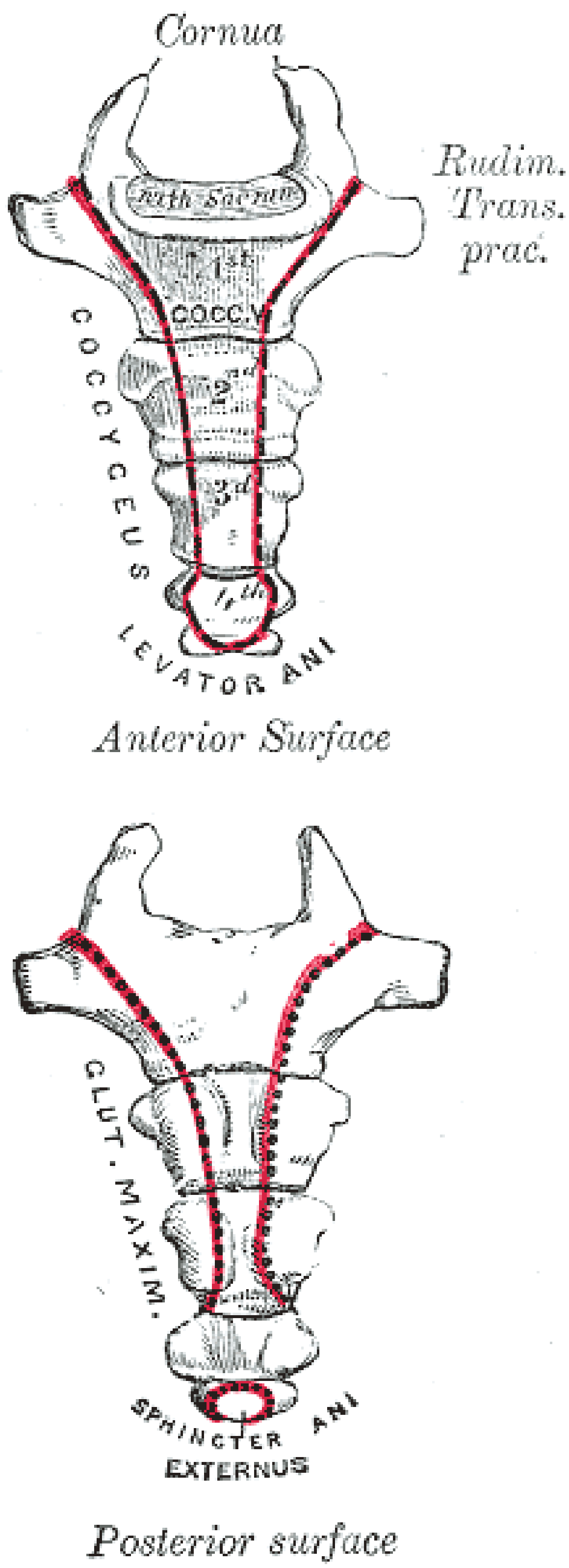

Figure 1: the coccyx

In x-rays, you can see where five vertebrae have fused together; the diagram shows the suture points, where the bones knit together as you grow. They start out separate, like our other vertebrae, but as we grow, they fuse into one chunk and don't grow as fast as our other vertebrae. This makes the vertebrae that form the coccyx sort of useless, but they remind us that our ancestors had tails, just like other mammals.

We call this a vestigial organ — a body part that is a vestige of a previous structure. Defining a vestigial organ is tricky, because organs like a tailbone are often not totally useless — they get reused by the body for new purposes. The key is that they do clearly show their earlier function. In the case of the coccyx, it is that clear fusion of these vertebrae, the coccygeal vertebrae, that lumping together as we grow of bones that would have been the start of a decent tail for our ancestors. The lumping shows us the bone is a vestige of our evolutionary past.

Truth is, we've got lots of these little traits in our body, weird design quirks that show us that the current function of a body part is a new app, a new deployment of a trait. We've got furry bodies, remnant of a lot hairy ancestors, and we break out in goosebumps when we're cold or scared.

Goosebumps are that fur standing up. Fluffing their fur when cold would have kept our mammal ancestors warmer. Back then, the hair was much thicker, and this fur would have trapped a layer of air, like a puffy insulated coat.

Puffing up when you're scared would have made you look bigger, more intimidating. Lots of animals try to look larger when they're threatened, hopefully so that they look less like a push over or an easy meal. Now, we've just got these mostly useless hair follicles that some us insist on tweezing off or 'manscaping.'

Some of these features are really 'vestigial' in that they don't seem to have a lot of use any more. Some people argue that our appendix is vestigial, left over from an earlier model of a gastro-intestinal tract. You can take a person's appendix out, and they survive pretty well. I should know, as I had mine removed twenty years ago. But some researchers think that the appendix is a back up organ to aid in the recovery from severe gastro-intestinal problems, a place where all the microbes in our guts that we need to digest our food right can hang out in case of trouble.

But perhaps an even better example is the little bit of muscle at the top of the ear. If you're sitting with someone, look at the top of the ear. In many, you'll notice one part of the top of the ear is slightly thicker than the rest.

You've got a bit of muscle there, but, because it's not connected to anything solid that it can pull on, you can't use it to move your ears around. If you could, you could hear better, shaping your ear to collect sound. Some of our evolutionary cousins can use that muscle to change the shape of their ears, to hear better, to communicate with each other, and to perform party tricks that we can only dream of.

Even structures like toes are vestigial to some degree, although they're useful for some kinds of things, like getting stubbed or wearing toe rings... or driving a car or braiding your daughter's hair.

Seriously.

We've got these digits on our feet that most of us don't use much. They're vestigial from our primate ancestors who could do all sorts of cool things with their prehensile toes, like climb and hold their children.

But the truth is that we could do a LOT more with out toes if we didn't box them up in shoes and let them get lazy. Some people, born without arms, or 'congenital amputees,' show us just what is possible, even with our short little toes — you can find examples of people playing guitar, driving cars, and caring for their children with their feet.

Stephen Jay Gould and Elisabeth Vrba (1982) wanted to call parts like our tailbones and body hair and toes 'exaptations' rather than vestigial organs. The word 'vestigial' sometimes gets taken to mean 'useless,' but that's not true of either tailbones or toes. Rather, tailbones and toes are 'exapted': they arise for one purpose, but they get repurposed, recycled or reused for some new function. Exaptation points out that evolution tends to be really good at putting old structures to new purposes rather than starting from scratch. In evolution, you never get a complete redesign; you always get a renovation.

How does the body do renovations? Well, let's go back to our tails. When I said you once had a tail, I was just talking about it vaguely, like 'you', 'you descendant of monkeys'. In reality, however, I'm talking about you, specifically.

Back when you were a little embryo about 30 days old, if we had good full-body pictures of you, you would have looked something like this. Yeah, I know, not exactly the baby picture you put up on Facebook is it?

You were only about 10 mm long back then, and more than 10% of your body length was tail — not five undersized fused vertebrae, mind you, but ten to twelve vertebrae in embryo as impressive as the ones that went on to form your spine and neck. In this cross section of the human embryo's tail (Figure 2), you can see clearly that it has all the precursor structures you would need to go on and form a fully functioning, waggable tail.

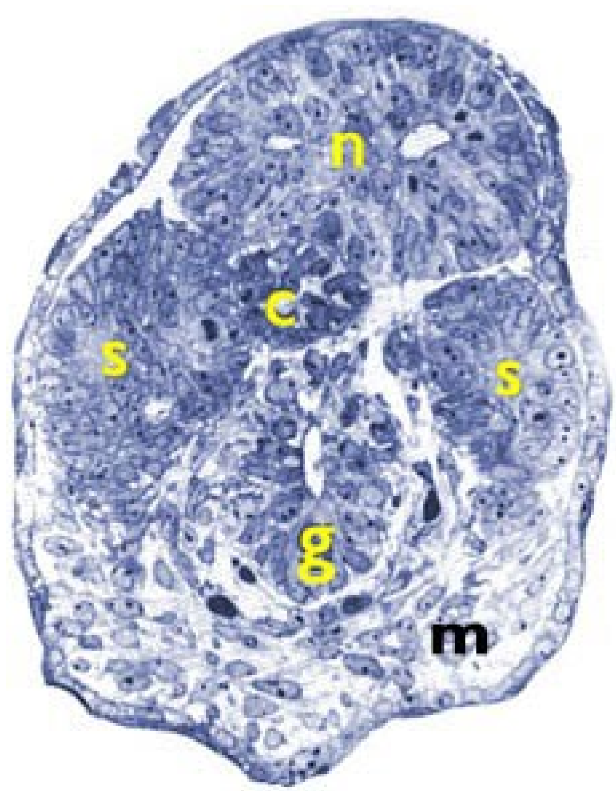

Figure 2: Cross-section of the human embryo's tail at Carnegie stage 14. Neural tube (n), notochord (c), developing vertebrae (somites, s), gut (g), and mesenchyme (m).

So what happened? Well, your DNA and the interactions of your cells eventually told your body to cut off those vertebrae, to starve them of resources, and the cells were reconsumed by your body, especially your immune system. The reason is that the genetic program to build you is quite similar to the ones that build other, similar animals, animals that do go on to have fully formed tails. The ingredients can be quite similar even if the instructions vary.

So, during human embryonic development, we have what could turn into a tail. In the bodies of many species of monkeys, similar vertebrae go on to be a fully-fledged, tree-branch-grabbing tail. But our DNA says, 'Nope. Scratch that. That's not in our plan for remodeling.' So we don't get a tail, and the body closes up shop on the whole tail-building project.

However, every once in a great while, the renovations aren't spotless, the instructions don't quite get transferred flawlessly. A slight difference in the developmental recipe leaves a bit of the tail behind, a bit of the tail that we all once had.

And then you get a fully fledged caudal appendage — an actual tail. They're rare in humans, really rare, but we've got a number of recorded cases. In this case, a posterior aspect of a neonate — that's science talk for 'a picture of a baby's butt' — shows a clear 2.5 cm or about a one inch tail. The technical name is either a caudal appendage or a saccrococcygeal mass because it's actually easier to tell a mother, 'Your child has a saccrococcygeal mass,' than to say, 'Sorry lady, your baby's got a tail.'

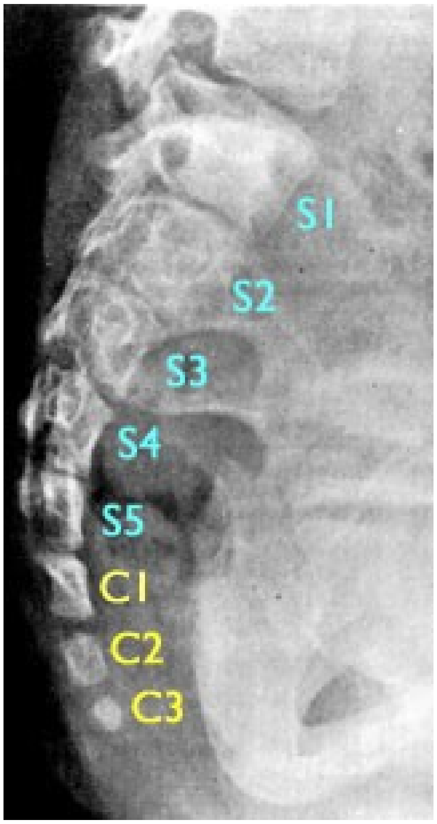

Figure 3: X-ray image of an atavistic tail found in a six-year old girl. Image reproduced from Bar-Maor et al. 1980, Figure 3.

And here's another great example (Figure 3): an x-ray of a 6-year-old girl with a full-on soft tail in the middle of her back. Normally, S1-S5 would have all fused during development in embryo into a little tailbone, about the size of S5 on this x-ray. Not only had they not fused, and gotten really large, but this girl also kept C1 to C3, part of those extra vertebrae that all of us have in utero but that disappear due to programmed cell death in the vast majority of people.

We call this kind of trait an 'atavism.'

An atavism is a sort of 'throwback'; it's the re-emergence of a trait that doesn't show up in the immediate ancestors, but was in a more ancient ancestor. It's not a new thing or some kind of innovative mutation. It's an old trait, a re-appearance, sometimes a very old trait re-emerging.

These cases are really rare. Atavistic tails — we probably have about 100 well-documented cases. So why should we care about them? Aren't they just freaks or mutants?

I don't think so. They're unusual, but cases of atavistic tails, like our own tails in embryo development and our vestigial tail bones — traits all of us have — show us that our bodies are littered with traces of our evolution. They are an example I'll return to next week when I talk about evolution and genetics because they show us two important things about how evolution makes us:

First, atavisms and vestigial organs and exaptations show us that evolution works by repurposing structures, using what it has lying around, not usually by making something completely from scratch. One of the main ways development does this is by tinkering a bit with the development program, cooking the basic ingredients — like vertebrae in a tail — in slightly different fashions. In one case, you get an underdeveloped and pretty useless vestigial tailbone. But in another related species, you get something else entirely — a magnificent tail that's useful for all sorts of things.

Second, traits like atavistic tails show us that we, like all life, have a lot of unexpressed genetic potential lying around in our body. Unusual cases like an atavistic tail remind us that some of these traits are there, dormant, maybe dismantled or checked by some developmental process, what biologists call 'unexpressed,' but that these developmental programs can still produce a trait, given the right conditions. That said, you're not going to get a tail just because you want one really bad, or because you buy lots of pants with extra space in the seat — you've got to get the right genetic material at the start.

This is one of the key points of studying human evolution. Human evolution is not just the story of an ancient past; it's also one of the only ways to understand the strange bodies that we have, especially these design quirks.

The biologist Theodosius Dobzhansky (1973) famously titled a short essay on the compatibility of science and theology, 'Nothing makes sense in biology except in the light of evolution.' When we look closely at the traces of evolution in our body, we realize how right he was. Only evolution can explain why you once had a tail..

Getting hands from paws

Some of the best evidence we have of evolution, in our own skeletons and tissues, is probably sitting right in front of you: your hands. On the one hand, human hands are so unusual; we can type and play video games, fight and climb and carry our children and even communicate.

On the other... hand, if we were to peel back the skin and look at the structure of our hands, we find that they were similar, strikingly similar, not just to the hands of our closest relatives — the other primates like chimpanzees and monkeys — but also to animals that might surprise us, like dogs, cats, horses, whales, and even frogs.

Biologists call anatomical similarities like these, homologies. Homologies are shared structures among species that are a result of evolution from a common ancestor. Even though two species may look quite different, even have contrasting abilities, when we look more closely at the internal configuration, the chemical and organic processes, the anatomy of organs, we find amazing similarities.

British anatomist Richard Owen, the man who gave the dinosaurs their name, from the Greek for ‘terrible lizard,’ and who established the British Museum for Natural History, originally defined the word ‘homology’ in 1843. Owen coined a lot of terms, most of which never caught on, but he’s also given us a few rippers.

Owen wrote that a ‘homology’ was the ‘the same organ in different animals under every variety of form and function.’ Anatomists of his day who systematically dissected animals found surprising structural similarities underlying different animals’ organs. When you peal the skin off, even of animals that look quite different, you often find that the organs match up remarkably well. The skeleton of a mouse and an elephant, a bat and a dolphin, often match up bone for bone, even though those bones have different proportions and functions. If you line up the teeth of the elephant with other mammals, for example, you find that the tusks actually match up to the incisors in other animals; they’re massively extended front teeth!

To get a sense for how homologies work, let’s take a look at my dog Louie’s front paw. From the photo, you might not think it looks much like your hand. He can’t pick anything up with it, can’t hold a pen, and certainly can’t open a can of dog food for himself. He mostly just runs around on it and uses it to scratch himself.

Figure 4. Louis, trusty dog assistant.

But if we were able to look at an X-ray of his paw, like this drawing, you would see some striking parallels with your own arm and hand (see Figure 5). Like you, Louie has a humerus connected to what we call our shoulder, and a pair of bones in the middle segment that match up to your radius and ulna. Louis has what looks like an extra joint in his leg that actually matches up very nicely to your wrist, with the carpals, or the wrist bones, and the metacarpals, which go from your wrist to your first knuckle in your palm. In Louie, however, the metacarpals, which seem like part of your hand, probably look more like part of his leg than his foot. Louis even has a little fifth digit — what's called a 'dewclaw' up a little ways on his leg. The dewclaw is a homologue to your thumb.

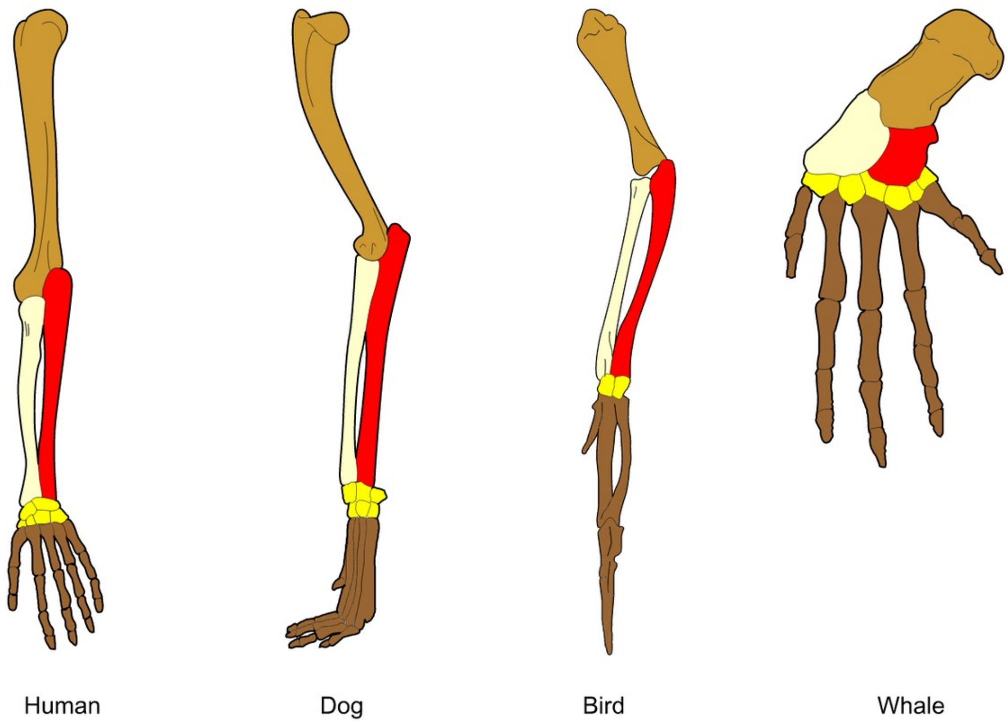

Figure 5. Homologies in the mammal forelimb.

If we look closely at a diagram, Louie's front leg is almost like seeing your arm and hand skeleton in a funhouse mirror, or using Photoshop to twist and distort the same basic collection of bones into a shifted configuration.

Even in a mammal with a radically different looking limb, like a horse or a dolphin, we find variants of this same basic skeletal anatomy (See Interactive 1.2). The structure is adapted to serve slightly different purposes depending upon the needs of the animal. Homologies are most impressive when we find similarities in what look like quite different structures descended from a common ancestor.

Figure 6. Jeffrey, chillin'...

This, for example, is Jeffrey (Figure 6). Again, Jeffrey's front leg doesn't look much your arm, but we find homologies with the human arm and the dog's leg. At the same time, we also see how, because of the way the limb has adapted, the changes are greater. With Jeffrey here, you have to realize that he's essentially standing on his middle finger, and that his middle finger (that is, his hoof) doesn't have all the joints that you or I have; he's just got one joint.

But he's got a humerus, a radius and ulna in the next section leading down to the knee or what is called in veterinary anatomy, the horse's carpus. The carpus contains a seven-bone configuration that is homologous to our wrist. The lowest part of the horse's leg, immediately above the hoof, is the 'canon'. It's homologous to the middle bone in a human palm, or the third metacarpal if you're counting in from the side. In the horse, this third metacarpal is fused with the neighbouring two bones (the second and fourth metacarpals in a human hand), like your five lowest vertebrae get fused into a coccyx. The fetlock, this lowest joint on a horse's leg, is like your first knuckle on your middle finger.

To get the bones of this leg and hoof, however, you really have to put those homologous structures we find in the human through some serious distortion. The phalange, for example, above the horse's hoof, is massive compared to the first digit in the human hand. Similarly, there's a lot of extraneous little bones in the human hand, so essential to doing what we do with our forelimbs, that never develop in the horse's hoof. Just like with the human tail, the developmental program of the horse's leg stymies the full development of these additional bits.

In contrast, in a dolphin's fin or a whale's front fin, you also find a pattern of homologies, but you see contrasts: the humerus, radius and ulna, for example, are all compressed to form a solid base for the limb when it's a fin. Whereas in the horse, the phalanges are simplified significantly, in whales and dolphins, the number of phalanges is multiplied, like they have super-long, multi-jointed fingers. In the bat's wing, again, we find the five digits, as well as the radius, ulna and humerus all stretched to support the wings. Here, the bat's individual phalanges are incredibly elongated relative to other mammals, because the surface area of the wing has to be so great, while still keeping the skeleton light. The contrast couldn't be marked between the dolphin's fin and the bat's wing, a result of one propelling itself through the air, and other needing to move through the much thicker medium of water.

Direction in the selection

In all the cases of homologies we talked about in the last section, we see how different species have taken a shared basic set of structures and adapted to a range of different environments and functions. Homologies show us clearly how evolution doesn't tend to make wholesale change, but rather, continually tinkers with structures and find ways to adapt them for new functions. Adaptation isn't about a perfectly engineered, special-purpose organ, but rather the gradual preservation of the best suited structures, and the development of better and better suited variants.

We call this 'directional selection.' When selection favours one extreme version of a trait, like a strong structure in a fin, or a light, elongated one in a bat's wing, that trait will get pushed in the direction of greater and greater specialization.

In the case of the tetrapod forelimb, that is, the front leg of four-legged animals, directional selection has driven different animals' structures in diverse directions, leading them to diverge in a wide range of ways. This kind of dispersal, we call 'adaptive radiation': a small set of animals is replaced over time by a larger set as clusters of the animal specialize and diverge in different directions.

We can also see how constrained adaptation can be by the process of directional selection and homology. Bats do not develop the ability to fly by growing a new set of limbs; their forelimbs are adapted for the purpose. So evolution can involve trade-offs. Is a change, on the whole, more likely to allow a species to survive and reproduce successfully because growing wings is going to cost the bat? If so, that variation will be preserved. But that doesn't mean evolution is like Santa Claus: it doesn't give animals presents out of the blue. It works one what they have, and is constrained by what is biologically possible. Tetrapods don't grow extra pairs of limbs (although these kinds of extraordinary changes can happen in some extreme cases).

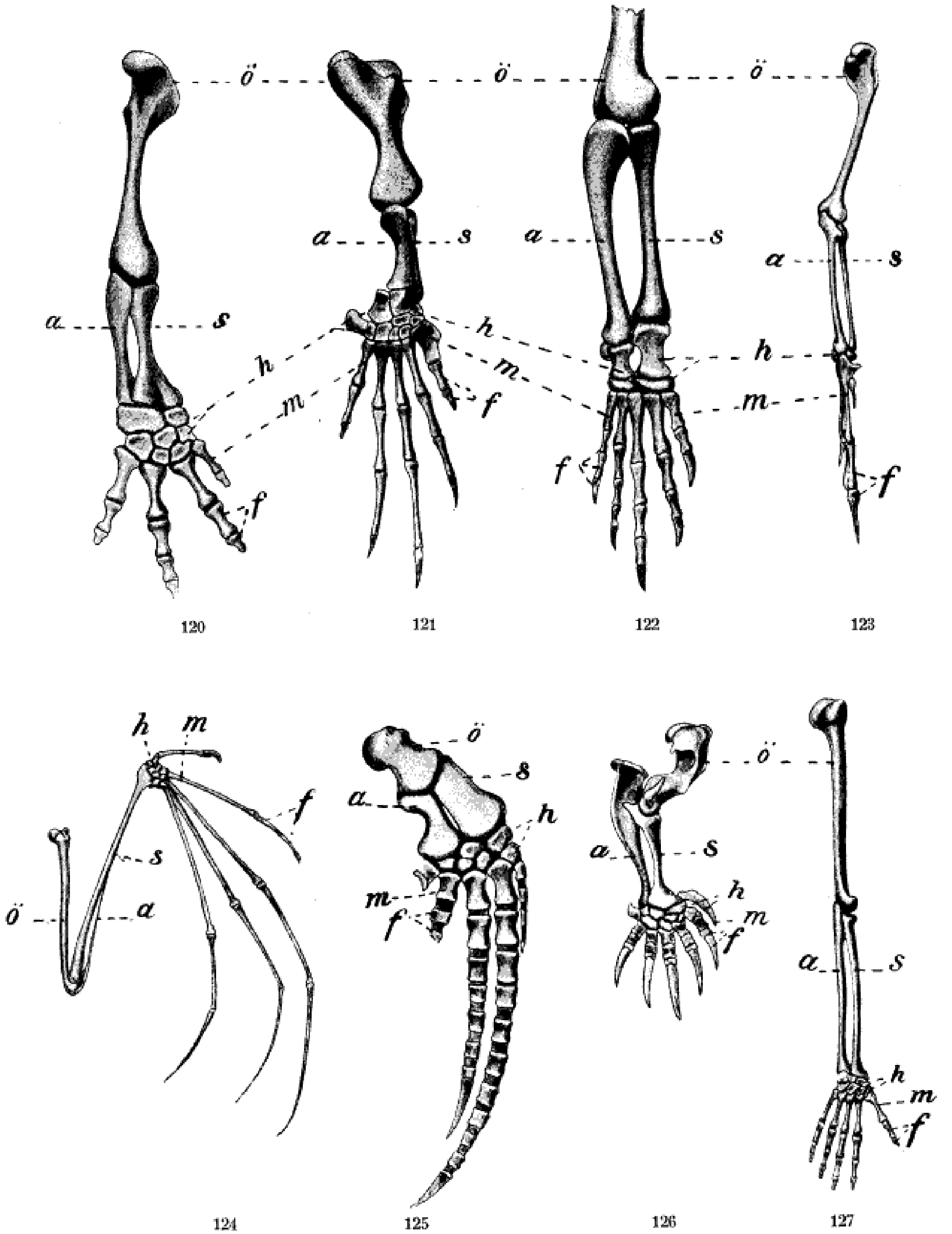

Figure 7. Homologies in a variety of tetrapod forelimbs. 120, salamander; 121, sea turtle; 122, crocodile; 123, bird; 124, bat; 125, whale; 126, mole; 127, human

Not every similarity between organisms is a homology; sometimes, the processes of evolution, including natural selection, produce traits through convergent evolution. Convergent evolution is a similarity that arises, not so much from shared ancestry as from selective pressures, sometimes even quite similar selective pressures. For example, even though wings in insects, bats, birds and pterodactyls developed quite differently, the demands of flight led to some similarities, such as their lightweight structure, strength, and flexibility.

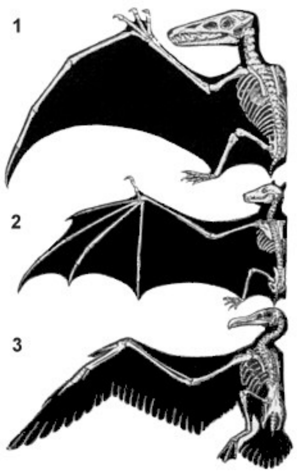

Figure 8. Convergent evolution in wings. The wings of pterodactyls (1), bats (2) and birds (3) are all light-weight with large surface areas, but their diverse structures show that they evolved these traits through convergent evolution.

Unlike homologies, when you look closely at examples of convergent evolution, you often find quite different underlying structures. For example, the structure of the wings of insects, birds, bats and pterodactyl are quite different: the pterodactyl has a bit of a claw on the middle joint because the wing is essentially a giant membrane stretched between the animal's body and a single, enlarged fifth digit. In contrast, a bat's wing has four digits with membrane stretched between them. The bird has yet another configuration with a simplified skeleton and feathered skin to increase the surface area; feathers actually decrease the need for the elongated digits in bats and pterodactyls. Flying insects are wholly different because they are such a distant relative of the other three, with no skeleton to reinforce their wings. Insects usually have two pairs of wings, composed of a thin membrane supported by veins.

These structures are analogues because they have developed independently, although the similarities between the tetrapods (the bird, bat and pterodactyl) and the radically different structure of the insect wing, shows you that the first three are more closely related.

Convergent evolution can produce fascinating examples of quite similar structures even in distantly related animals. For example, in Australia, placental mammals only arrived quite late in the continent's biological development, first just bats and rats, and later, tagging along with humans, the dingo and other invasives. Here in Australia, we have a wide range of marsupials that resemble non-marsupial mammals occupying similar ecological niches. For example, we have a marsupial possum, a marsupial mouse, a marsupial mole, we even had a marsupial predator, like the Tasmanian tiger which was a bit like a bobcat, and an extinct saber-tooth marsupial cat.

The similar pressures on these animals caused them to evolve in parallel ways to their counterparts among their distant cousins in the placental mammals. Although it's a little more complicated than this, as we'll discuss next week, this kind of evolution, where different paths lead to a similar destination, is an example of convergent evolution or an evolutionary 'analogue'.

In fact, the homologies across life can stretch much deeper. As our tools for genetic research have gotten more sophisticated, we now find that some of the genes underlying structures across virtually all of life are quite similar. In biological terms, they are highly 'conserved,' meaning that, even though they are in quite different animals, only distantly related, the underlying structure in the genes can be really similar.

One of the most interesting examples of this sort of deep homology are the genes that control overall structure of an animal, the Hox genes. The Hox genes specify which parts of the body go in what order. Although most genes are scattered around, the Hox genes are lined up pretty much in the order that they specify: the Hox gene that designates the mouth first, followed by the head, thorax, and abdomen. If a Hox gene gets duplicated in its genome, an animal often gets another copy of the body segment as the Hox gene basically runs the developmental sequence for that body segment an extra time.

We'll come back to it, but the Hox genes are basically the master control genes for body configuration, switching on cascades of other genes at the right times, making sure that an insect doesn't get legs on the top of its head, or a mouth in the middle of its abdomen.

Once geneticists figured out what Hox genes were in the 1980s, they went looking for them in a range of animals. What was striking is how similar the Hox genes were across a wide variety of species, even between simple worms and quite complex animals. For example, the Hox gene Pax6/eyeless seems to control the formation of light sensitive eyes in all species. There were differences, of course, such as the fact that mammals have four copies of the whole Hox sequence, but the toolbox of these genes tends to get used over and over again.

Although these discoveries have a number of implications, some of which we'll discuss, perhaps the most obvious is that they are the trace of our shared origins: the highly conserved, very ancient basic tools used to build all of the life we see around us. They are evidence that evolution has made a multitude of forms from simple beginnings. Charles Darwin suspected as much. In his book, *On the Origin of Species*, he wrote,...

"Therefore I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed." (Charles Darwin)

We are all related. Not just all humans, one to another, but all living things. Should make for a hell of a family reunion.

'Designed' by evolution?

The last bit of evidence for human evolution that I want to bring up this week is the 'blueprint' or 'design' of the human body. If you study the human body in functional terms, looking at how it works, it turns out that there are lots of design glitches that point to its evolution. The problems and flaws are telling, helping us to see the fingerprints of evolution; in a sense, they're just as interesting as the remarkable adaptations are.

In fact, I don't like using the word 'design' at all to talk about the human body, or any other evolved organism, because, to me at least, the word 'design' suggests that there's some kind of designer, some sort of plan.

Evolution has no plan. The body is not the product of a design, but rather of an organic process, over millions upon millions of years.

But before we get into that, let me show you what I mean.

First up, your eye, if it was 'designed', could be better. Probably the most obvious flaw is that the photoreceptors that detect light on the retina are all put in backwards. The layer of nerves that connect the retina cells to your brain aren't put where they obviously should be, if the eye was actually well designed: the nerves are inside the eye, covering the receptors, and not on the back of the eye toward the brain. So the light that gets to our retina has to pass through the nerves that carry the signal on to the brain. It actually makes our eyes less sensitive.

Moreover, it creates a real structural problem: all those nerve axons, as they come together in a bundle, have to get out of the eye in order to get to your brain. So you have a blind spot, a hole where the bundle of nerves goes out through the retina. Your brain tricks you, covering over the blind spot by stitching together a virtual image, like wallpapering over a flaw in your visual field with a bit of left-over information.

If you were a design student and you turned in the blueprint of the eye as your final semester project, your instructor would probably say, 'What are you thinking?' But the glaring design error of putting the retina in backwards is only one of the problems we have.

Our eyes could be so much better, more acute. For example, if we were sensitive to a greater range of light, we might see in the ultraviolet or infrared portion of the spectrum. Reindeer can see ultraviolet light, and important things like edible lichens, predator urine and wolf fur stand out for them in the same conditions that might make us snowblind. A bit more vision in the infrared part of the spectrum, and we've have night vision, the ability to see the light put off by heated objects, including living things. But we make do so well that we don't even notice the flaws.

Another flaw in the human body is the structure of the knee. No decent designer would put in a flimsy hinge joint on this weight-bearing limb, especially given that humans are bipedal, so we've got no spares. If there were a designer he (or she) would take one look at the specs for the job, the stress that the knee would have to endure, and immediately throw away the existing plan to bind together the joint with ligament. Back to the drawing board.

Every time you see a sporting event where some poor athlete goes down in a crumbled pile from a torn ligament at the knee, especially when they just tear it running or turning or stopping quickly, you should realize that no decent designer would try to hold together a knee with ligaments. The reason we have it though is because it's descended from a hinge joint in a fish's fin, where the flimsy construction would have been more than adequate.

The point is that you don't get what's best from evolution; you get what development and evolution can provide. It's good enough, or you wouldn't be here, but it's not the best possible structure.

It's often what engineers sometimes call a 'kluge,' a kind of improvised, overly-complicated, ad-libbed solution. The design is 'sub-optimal,' or 'less-than-perfect', but the key to understanding is to realize that it's not designed at all. That less-than-perfect-ness shows us how evolution produces structures by re-purposing or exapting earlier forms into new uses. Don Wise, a retired professor of geology who often argues with creationists says that, when the creationists want to talk about 'intelligent design,' he brings up these sorts of examples of 'incompetent design.

Getting evolution wrong

Another example of suboptimal structure is the whole genital area, especially in men (I'll come back to women in the sex chapter, so don't worry — I'm getting to you).

There's an old joke that no right-minded designer would ever put your waste disposal system right smack in the middle of one of your chief entertainment districts. The fact that you have sex and reproduce with some of the very same equipment that you use to get rid of waste is clearly not planned in advance. But that's not the only problem.

The way that testes get to where they need to be is also an exercise is jerry-rigging and ill-thought-out, or simply not-thought-out design. The testes start out developing in utero up in the abdominal cavity, but they can't stay there; they're homologies to a woman's ovaries, so both organs start in the same place. If the male testes were to stay inside the abdomen, however, they'd be too hot. The sperm would wind up defective from getting lightly cooked by a man's body heat.

So the testes have to descend to their eventual location in the scrotum. But to do so, they have to go through the lower abdominal wall. In the process, they leave two structural flaws in their wake, little weak points that can lead to an inguinal hernia. This kind of hernia is a painful and potentially life-threatening condition in which one of the flaws tears, and you can push some of your intestines out through the hole. Trust me, if you haven't had one (or two), the flaw is no laughing matter.

In addition, however, if this weren't enough of a problem — the whole waste-reproduction nexus, the descent of the testes — in men, the urethra runs right through the prostate. The urethra is the flexible tube that carries liquid waste out of us, and the prostate is a donut-shaped gland that tends to swell up over time. How's that for 'design'? Run a waste disposal pipe through an organ likely to swell over time and choke it off.

We could cite other examples: the fact that primates' bodies can't make vitamin C even though other mammals can, which means were susceptible to scurvy; too many teeth; badly designed spine; an extra cavity between the fallopian tubes and uterus where an egg can get stuck, leading to an ectopic pregnancy, we can go on...

But my last example is perhaps the most dangerous: human adults talk and breathe through the pharynx, the same pipe through which we eat and drink. Other mammals have this problem, too, but in humans it's much worse. As the larynx or vocal cords drop down the throat as you mature, the danger of getting food or liquid in your windpipe grows greater; this is why infants can nurse and breathe through their noses at the same time. The infant larynx is still high up in the throat.

But this design of the adult throat, with only the little epiglottis at the top of the larynx to avert constant disaster, means that we can die from simply eating and drinking while we talk. Evolution has come up with this kluge in part because we gain other advantages — the much greater range and control of sounds that we can produce as we grow into adults. It's bad design, but we're stuck with it because it produces other advantages, like a more versatile throat for making sounds, even deeper voices.

The reason I bring these flaws up is because I disagree with the way some people talk about the wonders of evolution. Sometimes, people — even me — will talk about how amazing evolution is because it produces wonderful 'design.' They will point to extraordinary traits of humans or other animals — birds' ability to navigate on long-distance seasonal migrations, the extravagances of mating, zombie ants with mind control fungus (no kidding), or the ingenuousness of adaptation — and they will say something like, 'Wow, evolution is a marvelous designer.'

I think that this way of understanding or describing evolution is dangerously close to believing that there really is a designer out there, some guiding plan or divine intelligence that is shepherding along all these creatures, shaping their structures according to a master plan.

In fact, living creatures are filled with bad design, in spite of their successful adaptation. The sub-optimal design, the less-than-perfect structures, show that the process is not being guided. No, evolution is tinkering with what's available. Here, evolution re-uses a hinge joint where another design would work better; there, it's stuck with a bit of muscle that's no longer useful; in another place, it uses a development process that leaves behind potentially fatal flaws.

Evolution doesn't give organisms the best design; it gives them tinkering and minor adaptations, sometimes structures or traits that defy good design principles, precisely because there is no designer.

This is important. Sometimes people think 'evolution' has a plan, or that it makes 'progress'. It's what we call the 'teleological error,' the idea that evolution has a 'telos' or goal. Sometimes people think this goal is increased perfection, or even that the telos is us, humans. You hear it being implied when people talk about one species being 'more evolved' than another, which is simply impossible unless it's sent back from the future where it's had more time to evolve. This kind of thinking can lead to people saying that humans are the 'most evolved' species, as if evolution where all some grand process leading up to us.

That's an anthropocentric view of the reality. It's totally natural, of course, just like assuming we're the centre of the universe, but it's not scientific. We may be the most intelligent or technologically advanced, but we are not the 'most evolved.' That expression doesn't even make sense. Every living thing is evolving all the time, sometimes in ways that make it remain unchanged over time, and sometimes with rapid change.

In fact, I would argue that thinking humans are 'more evolved' is actually a hold over of pre-evolutionary ways of thinking, especially of the idea of the Great Chain of Being. The Great Chain of Being was a Christian concept — other religions often have similar ideas — that humanity was the most perfect creation, just below spiritual or divine creatures like angels. For Christians, humans were God's most perfect material creation.

This way of thinking about our place in the universe has sometimes crept over into popular understandings of evolution, but it's not supported by the science. If we look at evolution, certainly, we stand out as unusual forms of life, but so do lots of other species. Which is 'best' or 'most evolved' depends entirely on the yardstick you use to measure. What we do know is that every living thing today has beating out tons of competitors for its niche; in that sense, it's the 'most evolved' for that niche. For now.

But there's no guarantee that, in the future, we or another species wouldn't follow the countless other species that have gone extinct before us, the 98% or more of all species that have gone extinct. We might get replaced by a new, tinkered-with version of ourselves or simply turn out to be the last in a 7 or 8 million year branch on the family tree of primates.

Studying human evolution requires a bit of humility: humility to recognize that we're far from perfect, humility to acknowledge that we are not rulers of all life simply because we've got some unusual quirks, and the humility to realize that our continued place in the web of life is far from permanent. There was a planet full of life before us; there's no guarantee that they need us to stick around.

References and Resources

Key concepts from the chapter:

The great mystery of human evolution is how the same forces that produced millions of other species, at the same, produced human distinctiveness.

Evolution has left its traces on modern human bodies — and all living things — both in the way that they are well adapted for their current niches, but also in the vestigial traces of past adaptations and in the counter-intuitive and overly complex adaptive traits.

Homologies demonstrate the way that underlying structures can be developed in distinctive ways over evolutionary time.

Often, evolution is misunderstood to involve ‘progress’ or striving for a goal; believing that evolution has a goal is a teleological error.

Resources:

African Fossils, a project of Louise Leakey and the National Museum of Kenya. Virtual lab with many virtual specimens. (link)

Human Evolution by the Smithsonian National Museum for Natural History. (link)

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The Multi-Dimensional Human Embryo. (link)

Douglas Theobald. 29+ Evidences for Macroevolution. Part 2: Past History. (link)

Greg Downey. Human (amphibious model): living in and on the water. Neuroanthropology. PLOS Blogs. (link)

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Holly Dunsworth, Evolution is the only natural explanation. And it's all we need. The Mermaid's Tail. (link)

Marcelo Gleiser, Why Do So Many Have Trouble Believing In Evolution?, NPR News (USA). (link)

P. Z. Myers, (2008) Hox genes in development: The Hox code. Nature Education 1(1), http://scienceblogs.com/pharyngula/2007/09/the_hox_code.php (link, more links here)

Sarda Sahney, Why does my baby have a tail?, Fish Feet. (link)

Neil Shubin, lecture on the discovery of Tiktaalik, a species linking aquatic "lobe-finned" fishes with early terrestrial tetrapods (YouTube). (link)

Kate Wong, The Most Fascinating Human Evolution Discoveries of 2012, Observation, Scientific American. (link)

Carl Zimmer, Turning Fins Into Hands, The Loom (weblog), Discover. (link)

Weblogs

There are too many good weblogs out there by anthropologists on human evolution, but here are a few of the ones that I consistently find great reading.

John Hawks' Weblog. (link)

Greg Laden's Blog, ScienceBlogs (topic: Human Evolution). (link)

Dienekes Pontikos's Anthropology Blog. (link)

Context and Variation, Scientific American, by Kate Clancy. (link)

Powered by Osteons, Kristina Killgrove. (link)

Patrick F. Clarkin, Ph.D. (link)

Ancient Bodies, Ancient Lives, Rosemary Joyce. (link)

The Primate Diaries, Scientific American, by Eric Michael Johnson. (link)

The Mermaid's Tale, group blog. (link)

Pop Anth: Hot buttered humanity! A collection of easy-to-read, fast-moving articles by anthropologists. (link)

Anthropology in Practice, Scientific American, by Krystal D'Costa. (link)

Carnival of Evolution is an itinerant, moving feast of links to new blog posts discussing new research in evolution. You can find links to the most recent edition, and prior ones, here. (link)

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Darwin

Charles Darwin's theory of natural selection was one of the most revolutionary ideas ever put forward, rocking our understanding of ourselves and our place in the world. It's been 150 years since the publication of *On the Origin of Species*. Although Darwin could not
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have anticipated all the discoveries that followed his work — research from fields as diverse as genetics and anthropology — natural selection is still the cornerstone of our understanding of evolution.

Charles Darwin sets sail

Charles Darwin, arguably, wrote the second most important book in shaping the Western world, second only to the Bible. Published in 1859, the full title of the book was, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* Today, we often refer to it simply as, *On the Origin of Species* or just *Origin*.

By the time he published it, Darwin was already a famous scientist and naturalist. He had been stewing on the ideas in *On the Origin of Species* for over two decades, afraid to bring them out for a whole host of reasons, including the potential repercussions of his ideas, repeated illness and family tragedy, and an intense desire to get it right, even if that required patience. His patience, what we might even see as timidness, seems really quaint today, when researchers often have PR people writing press releases heralding almost every lab result as a major discovery.

Darwin was not the first to describe evolutionary processes, to argue that species were not fixed, but that they changed and adapted. But Darwin's account, especially *On the Origin of Species*, seized the popular and scientific imagination in a way no previous work had. *Origin* set biology on a whole new footing, offering the first comprehensive account of the process we now see at the heart of evolution: natural selection. Darwin, however, was a reluctant revolutionary: he once told a close colleague that sharing his theories of natural selection felt 'like confessing a murder.'

Darwin's start wasn't terribly auspicious either: he was the fifth of six children, son of a wealthy society doctor in England and grandson of a famous naturalist, abolitionist and physician. He was sent off to Edinburgh Medical School to go into the family business, but he was bored by medicine, freaked out a bit by surgery, and wound up studying marine invertebrates instead: he discovered that the black spots on oysters were the eggs of a skate leach. He was much more interested in pheasant hunting season than his studies.

His father wasn't happy that he was neglecting his schooling, and so shipped young Charles off to Christ's College, Cambridge, to become an Anglican pastor. Darwin didn't do any better there, instead developing a passion for collecting beetles, a fad at the time. It may sound like an odd combination, but theology and naturalism were closely related in English thought at the time, as many naturalists looked to the natural world for signs of God's design.

When Darwin returned from summer break in 1831, about to grab his guns and head out hunting, he found that one of his professors had proposed him as the ship's naturalist for the HMS Beagle. The Beagle was set to embark on a journey around the world to map coastlines, especially South America, and Captain FitzRoy thought they needed a geologist and naturalist on board. Darwin was to be as much a companion to the captain as a scientist and collector, as the captain couldn't be expected to socialize with the crew during the long voyage (and the previous captain of the Beagle had gotten spectacularly depressed and shot himself). Although his father was grumpy about it, and thought the voyage a waste of time, a favourite uncle talked Darwin's father into funding his son's journey because Darwin wasn't even going to get paid for his work.

The Beagle departed in December on a five-year voyage. The ship mapped and charted coastlines. Darwin spent a lot of time on shore collecting fossils, biological samples, and geological observations as they went. When he recovered from seasickness, Darwin proved an excellent naturalist, observing coastlines in Africa, tropical forests in Brazil, and cliffs in Argentina. He collected marine life, lived through an earthquake in Chile, helped return kidnapped Patagonians from a previous voyage, saw the diverse wildlife of Easter Island and Australia and rode on horseback high into the Andes, hunting and exploring. Darwin didn't always realize the importance of what he was seeing — he ate the turtles that would later prove important to his theories about evolution — but he drew and wrote and collected as he went, sending back samples from his voyage.

Darwin's discoveries caused excitement among naturalists back home, as his samples and journals were shipped back ahead of the Beagle while it slowly circled the oceans for five years. By the time Darwin returned to England in 1836, his mentor had circulated his letters, and was eager to help Darwin organize to have all the samples analyzed. Some of the leading anatomists examined his finds: there were fossils of extinct animals from South America and a host of new species. Darwin's geological observations led him to argue that South America was slowly rising, and to put forward a controversial theory about how coral atolls, these fantastic circular islands, formed. Darwin's travel memoir of his voyage proved very popular and made him famous. He was a bit of a sensation and became a gentleman scientist, elected into the leading scientific societies of England, but mostly as a geologist.

But to truly understand the importance of Darwin, we have to look beyond his collecting. What made Darwin's impact so great was his imagination and grasp of the big picture, including the way that he read across geology, biology and even economics. He saw a pattern beyond the individual discoveries and samples. Darwin's greatest discoveries, in this sense, weren't on the Beagle; they were in the years afterwards as he wrote and read and gradually built up a theory that would embrace all of life, not just individual species.

As he voyaged, for example, Darwin read the first volume of English geologist, Charles Lyell's *Principles of Geology*, especially Lyell's theories of uniformitarianism. Lyell argued that natural forces were uniform across time. That meant that geological formations like valleys had to be explained by forces that could still be observed, working slowly over immense time rather than by one-off divine catastrophies. If geologists found fossilized seashells high in the Alps, as they had, either oceans were once much deeper, or the Alps had been pushed up, a little at a time, over countless years. Darwin was thrilled by Lyell's work as he now saw that the landscape told a story, telling how it had been formed.

When Darwin returned, he talked with the leading biologists of the day, too. They were already discussing the growing evidence that species could change or become extinct, once thought impossible if God had created each one individually. Darwin brought more evidence of species change, adaptation, and extinction.

The origin of On the Origin

To really understand how Darwin came up with his theory of evolution, you have to realize that he really wrote it after he came home. By 1838, he read the work of Thomas Malthus, *An Essay on the Principle of Population.* Malthus pointed out a grim fact of economic mathematics: populations could easily double each generation, whereas food production could not keep pace.

Darwin realized that species don't simply struggle against each other; the constant potential for excess reproduction, the enormous fertility of life, also drove species relentlessly, refining their adaptation. Darwin saw a relationship between the way farmers selected seed from the best produce to replant, the way that pigeon breeders chose which of their birds to cross-breed, and the natural process through which over-production could produce better adaptation. For this reason, Darwin eventually referred to the process as 'natural selection' because he thought nature, too, was selecting among that excessive fertility, like the pigeon breeders and farmers.

By the end of the 1830s and first years of the 1840s, Darwin was already thinking about a theory of natural selection, but he continued to focus on his geological projects: reports about the Beagle's collections, a book about coral reefs, work barnacles. He wrote a 230-page essay about natural selection, but he kept it secret, to be published only if he died before completing the work he wanted to write: he knew that reception was likely to be hard. His wife, Emma, a devout Christian, worried about the fate of his soul. But there were still problems that troubled him intellectually; he knew so much about diverse species that he kept analyzing more and more cases, reading widely and talking with other scientists, farmers, fishermen and animal breeders.

Darwin also struggled constantly with poor health, and was devastated by the death of his daughter, Annie. For twenty years he stewed on his ideas about natural selection, sharing them selectively with colleagues in his learned societies and scientific circles, building up a more and more massive case as he worked out his theories in notebooks dedicated to what he originally called 'Transmutation'.

Finally, in 1858, he was rocked by a paper shown to him by a young colleague, field researcher Alfred Russel Wallace. Wallace and Darwin had been corresponding, but Darwin was contending with an outbreak of scarlet fever that would eventually kill his infant son. Wallace sent Darwin a paper outlining his own theory of natural selection, threatening to scoop Darwin entirely. Fortunately for Darwin, two senior colleagues decided that the two should present together to the Linnaean Society. Even when the day came, Darwin was still too distraught to attend when the day came.

The 1858 presentation laid out the principles of evolution clearly, including parts written by both Wallace and Darwin; the audience included many of the leading biologists of the day. But the paper caused scarcely a ripple. In his annual report, the President of the Linnaean Society of London wrote:

'The year which has passed has not, indeed, been marked by any of those striking discoveries which at once revolutionise, so to speak, the department of science on which they bear.'

But then, in 1859, Darwin published *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. He originally wanted to title it 'An Abstract...' because it was a cut down version of the much bigger work he wanted to write. Luckily, the editor prevailed on Darwin to give it the shorter title. *Origin* was an unexpected best-seller, the first printing selling out immediately. The book went through six revised editions in Darwin's lifetime.

What made the difference between 1858 and 1859?

First, Darwin was a great writer, and his work still is rewarding to read. He saw in barnacles and beetles, seashells and orchids, peacocks and earthworms, a kind of grandeur. *On the Origin of Species* has a staggering breadth, and drew on examples that the broader population would know well, from the English countryside, farming and popular hobbies like pigeon breeding. Instead of a catalogue of life, description, now we have an explanation. Biology becomes an explanatory science instead of just a descriptive one, much like Lyell had showed Darwin in geology. But it took a scholar like Darwin, with his encyclopedic knowledge of life, to write a book with the kind of sweep that the *Origin* has.

The irony, however, is that in spite of his popularity, Darwin was still uncomfortable. Even though he we consider him the father of evolutionary theory, he didn't even like the word 'evolution': he preferred 'transmutation', and kept writing 'descent with modification' in *On the Origin of Species*. Darwin thought the word 'evolution' had too much of a sense of direction or progress.

Although his supporters fought fiercely on his behalf, the center-piece of *Origin*, the theory of natural selection, was still not widely accepted in Darwin's lifetime, and really wouldn't be for decades to come.

But his work was amazingly far-sighted. He foresaw some of the things we are discovering today, like the deep connections among all forms of life that we see clearly in genetic research. He pointed out that one reason that it is hard to see evolution is that 'descent with modification' is not a 'tree' of life, at all; it's more like a coral. The living species are like the surface of the coral, still alive, atop the skeletons of dead predecessors. We can't see the connections among the living because, like the hard structure under the coral, the connections are dead.

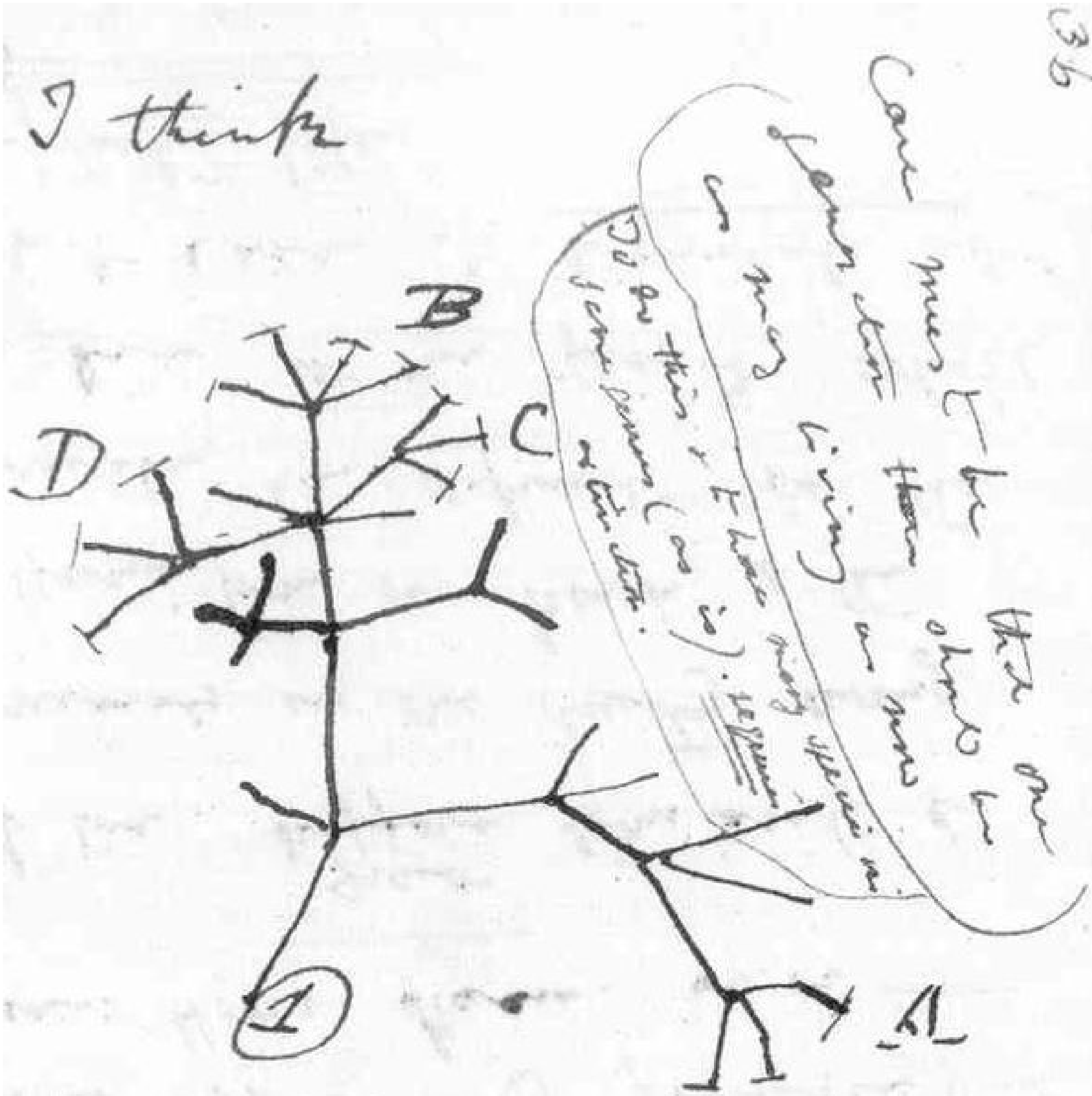

Figure 9. Charles Darwin's 1837 sketch, his first diagram of an evolutionary 'coral' from his notebook

But ultimately, one of the reasons for the success of *On the Origin of Species* is because Darwin himself was so fascinated with the range of life, the astonishing way that species can adapt and change. Like the natural theologians, who saw the fingerprints of God in the majesty of nature, Darwin still had the capacity to feel awe and to share that with his readers.

At the end of *On the Origin of Species*, he shares this vision:

'It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. . .

There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone circling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.'

Natural selection

How does evolution work? Let's take an example that we know is going on because it's happening right in front of us (and causing doctors all sorts of headaches).

In our hospitals right now, we are breeding super-bugs, strains of bacteria that are so resistant to antibiotics that they produce hard-to-cure, even potentially, life-threatening, infections. For example, there are now forms of staphylococcus, a bacteria that lives normally on your skin and in your sinuses, that are not susceptible to penicillin; there's even some varieties of staph that are resistant to multiple different antibiotics.

These varieties of the antibiotic evolved because, when they were doused with penicillin or other antibiotics, those bacteria without resistance died. Left behind were the lucky — those who just missed contact — or those bacteria with a bit of resistance. Over time, the use of antibiotics made the population of bacteria more and more resistant by slowly wiping out any bacteria that had vulnerability to the drug.

Staph evolved antibiotic resistance, not because it wanted to or because we wanted it to, but because penicillin and other antibiotics slowly changed the population of bacteria, making it more and more likely that vulnerable bacteria wouldn't make it to reproduce and pass on their traits. Without the drugs, this trait wouldn't have been that important. With the invention of penicillin, suddenly, whether a bacteria could survive being doused with it became crucial to its survival, and to the evolution of the species.

Natural selection is the key to understanding evolution. The principle is deceptively simple. What makes natural selection most difficult to understand, I would argue, is that we tend to assume that the theory is saying things that it is not. One way to understand it better is to see how you can get it wrong.

One of the most widely-accepted explanations for species change before Darwin, held even by many of Darwin's followers, for example, was the theory of French naturalist Jean-Baptiste Lamarck. Lamarck believed in the inheritance of acquired traits. That is, if an animal or plant acquired a trait through use, or if a trait atrophied because of neglect, the change could be passed on to offspring.

An example of Lamarck's theory goes like this: If your father did hard labor and got strong from it, you would be born with bigger muscles; he passed on his acquired strength. The blacksmith's son would allegedly be born different than the shopkeeper's because of the parent's occupation. In the classic example used by Lamarck, giraffes had long necks because the ancestors of modern giraffes had stretched and stretched up to eat the high leaves on tree branches. A trait became exaggerated through use, even through aspiration or desire — like the giraffes reaching and reaching.

On the other hand, disuse led to atrophy and the potential loss of a trait. Lamarck and other naturalists knew that people grew weaker from inactivity; they just thought that this could be passed on to an animal's offspring.

In contrast, natural selection is deceptively simple. The process is, in four words: *Nature proposes. Selection disposes.*

Darwin realized, from reading the works of Thomas Malthus, that population growth was potentially geometric. Many more individuals were born than could survive and reproduce; two human parents could easily produce four, five, six, even more children. In other species, the potential growth rate was even more staggering. This constant increase in population inevitably butted up against limits in habitat, food, and other resources. This meant that there was always competition within a species, just as there would always be predators, diseases, climactic change, and other forces of nature. Resources were limited; life was potentially abundant.

In addition, living things vary. You do not look exactly like your siblings; more importantly, you do not have the same abilities, traits or potential. You might even have different resistance to disease. Members of the same litter of kittens or the same clutch of eggs are not identical clones of each other. If every member of a species cannot survive to reproduce, or reproduce as successfully, and they varied constantly, some variations might be more successful than others.

By whatever mechanism — Darwin didn't know anything about genes or mutation — natural processes produce abundant varied life; the growing population together with a whole range of challenges — finding food, staying safe, surviving the elements, finding a mate — sorts that variation out. If the variation can be inherited, and that's key to why Lamarck was wrong about a lot of things, and the selective pressure continues over time, slowly, the variants with better chance of survival and reproduction will grow more and more common. A species will change and adapt by shifting toward one of its extremes, if that extreme is more likely to survive generation after generation, like the staphylococcus becoming resistant through generations of exposure to deadly penicillin.

If there's no variation in a species — if they're all identical clones — then there's no natural selection. Natural selection *requires* variation. Also, if there's no selective pressure, there's no evolution. That's sort of harder to imagine, but it comes up in the sense that some situations are more or less intensely selective: super-high fertility and really high mortality rates can set a species up for rapid evolutionary change. In times of great hardship and mortality, selective pressure increases.

The expression 'survival of the fittest' is sometimes used to describe natural selection, and that's a good enough way to think about the process as long as you understand what is meant by 'fitness.' 'Fitness' doesn't necessarily mean the 'strongest' or 'biggest' or 'meanest' or even 'healthiest' survive. The idea of 'fitness' is quite subtle; individuals often don't compete directly with each other (although they sometimes do).

Which individual is ‘most fit’ depends entirely on the selective pressures. Whatever forces are most likely to prevent an individual from successfully producing offspring, these are the selective forces. They can be predators, difficult to digest foods, competition from another species, changes to the environment, diseases, competition to mate, surviving lean periods and lasting through to mating season... Whatever force threatens you, your ability to reproduce, or your offspring, that determines which variant is ‘most fit’ and which trait is under pressure to produce adaptation. In staph, it’s been resistance to antibiotics, which didn’t matter before the discovery of these drugs.

Another example: if a species is subjected to periodic famine, if the factor most likely to stop an animal from reproducing is dying of hunger during a dry season, this pressure would favour those individuals who are adapted to surviving near starvation. They are the ‘fittest’. The pressure could favour the ones with the slowest metabolism, those able to pack on reserves of fat, or maybe even a variant than just goes to sleep for long periods in a safe place to avoid starving.

Different species sometimes compete head-to-head for the same resources. We call this inter-species competition, like when two species of predators hunt the same food source. Inter-species competition tends to lead to extinction of one specie due to competitive exclusion; one species is inevitably going to have an advantage, and unless the less competitive species can find a niche where it turns the table and hang on, it’s liable to disappear.

Natural selection (part 2)

Most evolutionary change, however, is driven more by intra-specific competition. The dynamic is not so much bats vs. flies, for example, but more among bats with all their variation as to which bat will be most successful in getting food, reproducing, and supporting more offspring. If flies get faster or evolve to better avoid bats, they won’t replace the bats in the ecological system; faster flies will put more pressure on bats, making it harder for them to get food, perhaps driving bats to evolutionary change.

If you have competing directional selective pressures, you can often get long periods of what look like no evolution, no change. Species can be very stable if they undergo stabilizing selection. For example, it might make sense for a primate to get larger to compete to reproduce, but at a certain point, the increased size might lead them to struggle to get enough food, find tree branches strong enough to support their weight when hiding from tigers, or even keep cool, because big bodies have more of a problem with over-heating. Body size might hit a kind of adaptive sweet spot, remaining consistent over long periods. The trade-offs involved may make a compromise between the two directional tendencies optimal, and pin down a trait for long periods of time.

Natural selection can also lead to species change through directional selection. Directional change occurs when an animal can gain advantage by a trait becoming more exaggerated. If short-necked giraffes can’t compete as well for food, they tend to die out, leaving only longer-necked giraffes behind. In some cases, if selection keep eliminating the shortest, the remainder get taller and taller until they hit some biological constraint or a stabilizing point.

If you have competing selective pressures on a species, you can also produce diversifying selection. The population may split, with those at each extreme better able to survive and reproduce than more average members of the species. For example, for mice or rabbits living in the arctic, being very lightly coloured to blend in with snow and ice makes some animals 'more fit.' They are camouflaged and less likely to be spotted by a predator.

The same colour pattern, however, is a real disadvantage if the animals lives in a temperate climate, such as grasslands or a forest, where white fur will make the animal stand out. In these areas, dark brown mice may have an advantage. In both settings, intermediate coloured mice might be less well camoflauged, so they disproportionately wind up getting eaten by owls or hawks. In the end, you can wind up with two separate populations, one very dark and one light, each adapted to its environment. Given enough time, if you keep them apart, and you'll find that they turn into two separate species, what we call speciation.

Diversifying selection can actually happen in multiple directions, into multiple niches, in a pattern called adaptive radiation. A basic rule of thumb is that, if you see a pattern of multiple species arising from a single ancestor type — diversification — you know that the new variants are occupying different niches, maybe even dividing up the resources, finding new ways to live, and specializing.

For example, all mammals alive today have descended from a common shrew-like ancestor that lived in the shadows of the dinosaurs for almost 150 million years. With the extinction of the dinosaurs about 65 million years ago, a whole lot of niches opened up for mammals to fill, and our ancestors diversified into thousands of forms. As the number of mammals increased, there even developed a niche for mammals that ate other mammals. Over the next tens of millions of years, directional selection for a whole range of different environments — mammals that dug under grounds, mammals that lived in the ocean, mammals that hunted at night, mammals that ate grasses — produced an explosion of adaptive radiation. Thousands of species.

To sum this up, natural selection is kind of like an equation:

(Variation + Inheritance + Selection) over Time = Adaptation

We can abbreviate this as VISTA to help us to remember. If any of the first four is not present, you can't have natural selection. For example, if there's variation, but it's not inheritable, then it can't really be the target of natural selection. It can change, but it's not from natural selection. Many people argue that this is why culture and technology don't really undergo natural selection, although they change and develop over time. You don't inherit technology in the same was as a genetic trait: you don't inherit your parents' education, for example, or their inability to understand how their new phone works (so that's a good thing!).

If there's not variation sufficient to create some kind of selective advantage or difference in fitness, there's no natural selection. If a trait in an animal is uniform, selective pressure on it can't make some more likely to survive than others. As Charles Darwin wrote in 1868, in his book, *The Variation of Animals and Plants Under Domestication*, it doesn't take much: 'slight individual differences, however, suffice for the work, and are probably the chief or sole means in the production of new species.'

No diversity; no evolution. This is one reason that the idea of a genetically uniform 'master race' doesn't make evolutionary sense. Our evolutionary insurance policy is our diversity.

Without sufficient time, natural selection can't bring about change. Or if conditions change too frequently, then natural selection can't apply directional pressure long enough to produce adaptation.

How fast can evolution happen? Well, that depends, especially on the severity of the selective pressure and the rarity of the trait that confers an advantage. Some theorists thought evolution was probably pretty slow, but we now have examples of changes happening relatively quickly. One of my favourite examples is the case of the size of snakes in Queensland since 1935.

In 1935, the cane toad — *Bufo marinus* — was introduced from Hawaii to Queensland by sugarcane farmers who hoped that the toad would eat a type of native beetle that fed on their crops. The experiment was one of the great disasters of human biological engineering. Not only did the cane toad have no effect on the beetles, but the toxic frogs started to cause a decrease in the native fauna, like quolls and even goannas and other reptiles. They were incredibly fertile; a female *B. marinus* can lay up to 25,000 eggs at a time.

The cane toad is a huge threat to biodiversity as most native animals like reptiles think that it looks like food, but it's loaded with venom, bufotoxin. One of the casualties has been the local snakes. Eat a cane toad, and a snake is liable to die. There are so many of the toads that virtually every snake will come across one and try to eat it. The only snakes that were safe were those too small to eat the hulking toads: a form of intense directional selection. Being large was virtually a death sentence as the snake found a cane toad lunch irresistible. In less than eight decades, the introduction of cane toads changed the size of snakes by introducing a new selective pressure.

The new variant of the snake was not an unprecedented mutation; it was just the runts of the litter, the extreme of the species' normal range. As large snakes died before they could reproduce, their trait started to disappear from the population. Directional selection concentrated and exaggerated the small size.

Some evolutionary theorists call this kind of pattern 'punctuated equilibrium.' A species might exist at a kind of 'equilibrium' under stabilizing selection, with natural selection favouring consistency generation after generation. A new selective pressure caused a kind of 'punctuation,' a rapid change to a new equilibrium, like a crash in the average size of snakes that stabilizes once they are too small to eat the poison cane toad. The pattern explains what we often see in the fossil record: long periods of consistency in some species, interrupted occasionally by fits and starts of change.

Natural selection was happening all along; it's just easier to see its effects when the situation changes, and the selective pressures shift. Upheaval is more likely to produce change, whether that upheaval is imposed on a species by external conditions, or whether it comes about because of some change in the species itself.

Genetics

Charles Darwin's theories were only partially accepted in his lifetime, even by some of his fiercest supporters. Darwin convinced fellow naturalists that species changed, he even convinced a lot of the public. But Darwin's contemporaries, even his supporters, didn't necessarily accept his argument that natural selection was the primary force. They couldn't see how *slight* variations in a population, causing *slightly* different chances of survival could, over time, add up to *major* change. The most innovative, and arguably most important part of his theory was generally disregarded.

One reason is that Darwin couldn't explain how inheritance and variation worked — *no one* could at the time. Darwin, like many of his contemporaries, thought that offspring had a mixture of the traits of their parents.

The problem is, if inheritance is just the mixing of the traits of the parents, then over time, we would expect overall variation to decrease constantly in sexually reproducing species. Any unusual plant or animal couldn't pass on its unusual trait fully to its offspring because that trait would be constantly diluted by mixing with another, more normal parent's traits. Worse still, if all offspring are a mixture, then all offspring would be alike. So variation decreases by half in each generation because two different parents produce a group of intermediate and identical offspring.

Imagine that all the variation is different colours of paint: if you start mixing the paints and you keep mixing randomly, time after time, generation after generation, you eventually wind up with a collection of muddy brown mixed paints. The idea of the mixing of traits seemed to predict the same outcome — less and less variation. The problem did not escape Darwin or his critics; one early reviewer of *On the Origin of Species* pointed out the problem: how did inheritance produce variation?

The problem was not with evolutionary theory or natural selection, but with the very idea that inheritance was a blending of traits. We wouldn't understand how inheritance and variation worked until we learned about genetics.

At the same time that Darwin was working on his many projects, a German researcher and friar, Gregor Mendel, was studying the reproduction of peas, working on what turned out to be the solution to the problem of decreasing variation.

Mendel planted thousands of pea plants in an experimental five-acre garden at his monastery. He wanted to understand how inheritance worked, so he carefully controlled how these plants fertilized each other, mixing pure varieties to see how the hybrids would turn out. His project was unprecedented. In less than a decade, he planted, carefully fertilized and meticulously examined almost thirty thousand pea plants. His results were surprising, so much so that he wasn't recognized until long after he had passed away.

Mendel discovered that the plants reproduced in a fixed and predictable way: if he crossed two pure varieties of the pea plant, each with a contrasting trait, all of them would predictably take on one of the parent's traits. Cross pure-bred plants with contrasting smooth and wrinkled-skin peas, for example, and you always got a smooth pea off-spring. We call this the dominant trait because, when the two are both present, the dominant trait gets expressed. In this case, the smooth skinned pea variety is dominant.

However, and this is where it gets interesting, if you take these second generation plants, all with smooth peas, and cross them, you get something unexpected: three-quarters of the plants have smooth skin peas and one quarter have wrinkled. So the smooth-skinned second-generation plants are carrying, unexpressed, the trait that produces wrinkly skin or they couldn't pass it on to the third generation. Keep crossing these hybrid plants, and the non-dominant variety keeps popping up. The trait can skip a generation. The ratios in each generation were crucial, because Mendel could work out that two different variants together were causing the distribution (see Figure 2.20 for an explanation using red to represent the dominant trait).

Mendel realized that the plants were getting what we now call a 'gene' from each parent, but the presence of the dominant allele, or gene version, was masking or hiding the other allele, which we call recessive. The traits were not really 'mixing.' They were being passed intact to the offspring, lying in wait if they were ever to mix in an offspring with the same recessive trait from the other parent. Variation didn't necessarily disappear, even if it went underground.

This pattern is particulate inheritance, as opposed to mixing: you either get the gene, the 'particle' that determines this trait, or you don't.

The simplest example of particulate inheritance is sexual reproduction itself; in the vast majority of cases, a child does not wind up a 'blending' of the father and mother's sex. Bodies are typically either male or female (with some exceptions we'll talk about in week five). You either get a Y chromosome or you get an X; you don't get a mixture of the two (although, as you'll often find in biology, it can get more complicated than this and there are almost always exceptions).

Mendel read a paper about his research at the time and published it, but it only got cited a few times over the next three decades. Mendel got promoted to head of his abbey and gave up his pea plants. What Mendel had discovered, however, were two key findings in addition to particulate inheritance which we now refer to as the 'laws' of Mendellian inheritance:

First, every individual possesses two copies of the gene for a trait, but only passes one of these along during sexual reproduction; a child gets one from each parent. You only pass on half of your genetic material to your children if you reproduce sexually. If a hybrid parent passes on a recessive gene, and it gets together with another copy of the same gene from the other parent, the offspring can have a recessive trait that was being carried, unexpressed in both parents.

Second, Mendel recognized that traits ‘independently assort,’ that is, you don’t get all your traits from one parent or the other, or a blend, but different discreet traits from each parent. Not all smooth skinned pea plants are tall and have big leaves and purple flowers; each trait is determined independently during sexual reproduction by which ‘particle’ of inheritance you get.

Only some traits behave precisely in the way that Mendel described because many traits are, in fact, polygenic; many genes affect them. For example, your skin colour is affected by multiple genes. Mendellian traits, that is, those determined by a single gene pair, tend to be ‘discrete’ traits: either you get them or you don’t, with no real in-between. In contrast, many traits are ‘continuous’ and affected by multiple genes — for example, skin colour comes in many, many shades, light and dark and everything in between.

The ‘modern synthesis’

The German evolutionary biologist August Weismann rediscovered Mendel’s work when he was proposing his germ cell theory of inheritance. Weismann argued that inheritance only happened from parent to offspring through the germ cells: the father’s sperm and mother’s egg. Nothing that happens to the bodily cells during your lifetime could affect the germ cells, which produced body cells in your offspring. Transmission was one way; from parent to child through germ cells, and from germ cells to body cells.

What came to be called the ‘Weismann barrier’ meant that acquired traits could not be passed on. The children of a weightlifter were not born extra strong. Lamarck was dead wrong, according to Weismann.

To prove it, Weismann removed the tails of mice, and then of their offspring, over and over again for multiple generations and yet every successive mouse was still born with a tail, demonstrating that acquired traits — in this case, being tail-less — were not inheritable. We now know that this is more complicated, but Weismann’s ideas were crucial for shaping research in genetics and for helping to seal the acceptance of natural selection as the mechanism driving evolution.

By the early 1940s, biologists across a wide range of fields, from genetics to evolutionary theory, could begin to see their work flowing together in what Julian Huxley called the ‘modern synthesis’: that synthesis was the hybrid of Darwinian natural selection with Mendel-inspired genetics.

According to the modern synthesis, to understand evolution, you had to focus on the population as a whole, over many generations, not any one individual, nor any single lifetime. Evolution was working slowly on a background of genetic variation in a species, on the whole population, not on any one individual. Individuals lived and died, successfully reproducing in some cases, passing on the genetic material in their germ cells. What you did in your life didn’t really matter to evolution — it wasn’t affecting your germ cells — except if you reproduced a lot, a little, or not at all.

Natural selection, over time, was shifting the total genetic profile of the whole population, the gene pool, making the most fit genetic types gradually more and more pervasive. If having wrinkly skinned-peas made a pea plant more successful, the gene pool would slowly get filled up with that variation, squeezing out other, less-successful varieties.

The discovery of DNA helped to confirm that biologists and evolutionary theorists were on the right track. DNA or deoxyribonucleic acid is a complex organic compound that can store information inside of living cells; it's found in the nuclei of all living cells, and even some viruses.

DNA is a very long molecule that looks like a twisting ladder, what biologists call a 'double helix'. The sides of the ladder are made up of a sugar-phosphate chain, but the steps are what is crucial: the steps are base pairs of four different nucleotides, compounds which are used in the DNA of all forms of life. The nucleotides are like four letters that provide a code or pattern for building amino acids, which can then be assembled into proteins to do all the sorts of things that cells need to do to live. The DNA molecule itself is huge, with over three billion of these steps, the base pairs, on the human chain.

Geneticists realized that variation could arise if that code was not copied successfully. When the DNA molecule unzips so that it can make two copies of itself, a mutation or a change can be introduced to the sequence that might cause a new variation, even something entirely unprecedented to arise. A part of the sequence could get accidentally inserted, left out, copied twice, turned around the wrong direction, or any other sort of DNA clerical error. Genetic mutation provided an important way to understand how variation could arise; most were harmful, but some mutations might actually be beneficial.

For example, we know that humans developed dark skin as we lost our hair in Africa; the dark pigmentation protected our ancestors from over-exposure to ultraviolet light, protection that we lost as our hair gave way to make it easier for us to cool our bodies. At least three times since then, a mutation or genetic change has caused a population of humans to develop much lighter skin: at least once in Neandertals, once in Europeans and once in north Asians. A slight change in the genes linked to the production of melanin, or the dark pigment in our skin, has proved to be an important change for surviving in northern latitudes, where some of our ancestors got much less light, and would have struggled to produce enough vitamin D to stay healthy.

That genetic code is crucial; sequencing the code has been one of the greatest scientific achievements of the last twenty years. But it's also produced some real surprises.

First off, in 2003, when the first human genome was sequenced, and researchers were in for a bit of a surprise. Back in the 1960s, some scientists thought that the human genome might have as many as 200,000 protein-coding areas. The number turned out to be only about 21,000 or so sections that we had patterns for proteins — about the same number as the mouse. A lot of the DNA — about 98.5% — didn't seem to be active at first glance, and some scientists started referring to it as 'junk' DNA. We now realize that, in fact, this DNA is quite busy, regulating and affecting how and when the DNA sequences that code for proteins go about their work.

DNA, by itself, doesn't do anything. In fact, it can sit quite happily for a very long period of time; that's why we can pull it out of a crime scene or even out of a bone of a long-dead ancestor, in some cases. The cell itself has mechanisms for expressing different genes, or preventing a gene from being expressed. This clearly happens in multicellular animals where every cell has the same nuclear DNA, but they do very different things: bone cells and muscle cells and brain cells result from the same DNA being expressed differently.

Some of the inactive sections of our DNA are 'pseudogenes': sections of DNA in which a mutation has knocked out the function. For example, humans have a large number of areas of genetic material that look like the areas, in some species, that cause the olfactory system to form in sophisticated ways. These genes appear mutated in us, so that they don't serve the same purpose that they do in other species.

Some of the variation in the human genome also arises from copy number variation: multiple copies of the same section of a DNA strand. Even identical twins can differ genetically because they get different copy numbers of some sections of the same DNA.

We don't really know how all the variation works, although geneticists are making enormous advances every year in helping us to better understand how inheritance and variation both work. These discoveries are not over-turning natural selection, by any means, and the vast majority of evolutionary theorists will still argue that it is the central mechanism that is, over time, shaping the traits of all living species, including humans.

It may be hard to believe, but some of the most important parts of being human have nothing to do with our consciousness or intelligence or even our intentions or motives. Being human means passing on your genetic material or not, being part of a pool of genetic material, constantly shifting and being tested by natural selection, never identical from one generation to the next, even if you have absolutely no idea that it's going on.

Epigenetic inheritance

In 1944, near the end of World War II, the Nazi army cut off supplies to the occupied Netherlands to punish the Dutch for hindering German war efforts after D-Day. The harsh winter of '44 to '45 became known as 'Hunger Winter' as food and fuel ran out, leading to a brutal famine until spring brought a thaw and resupply by Allied forces.

The mothers who were pregnant during Hunger Winter gave birth to infants that were smaller than usual, and these infants were also more prone to certain health problems later in life, like diabetes, cardiovascular disease and obesity. That was interesting, but not a huge surprise.

What was more surprising is that the children of these children, born decades later, were also more prone to certain health problems. Animal studies have confirmed that a grandparent's response to starvation can, in some cases, influence how their grandchildren will develop. Increasingly, biologists are convinced that some acquired influence can affect an individual's offspring; the question is, what sort of influences, how important are they, and through what type of biological mechanisms?

The 'modern synthesis' focused almost entirely on genetic inheritance. Some proponents were absolutely steadfast: only genes could be inherited, nothing else. More importantly, because only genes were stable over the period of time needed for natural selection, other forms of inheritance didn't matter even if they did happen, or at least they couldn't 'evolve' from natural selection.

Some advocates of the 'modern synthesis' went so far as to take a kind of 'gene's view' of evolution. They argued that, because inheritance was genetic, you could model evolution, not as a struggle for survival among organisms or between species, but among genes themselves.

There's some truth in this gene-level perspective, and it's a necessary antidote to some popular misunderstandings of how evolution works. For that reason, I think it's important. In a way, though, it's kind of like economics: it's a powerful way of looking at the world, a way of blocking out a lot of confusing distractions and homing in on the primary dynamic of evolution, which is genetic change of a population due to natural selection. But the problem is, biology is seldom so simple.

Increasingly, evolutionary theorists are realizing that the modern synthesis needs to be expanded to include the recognition of other mechanisms of inheritance — not just genes. Our VISTA model of natural selection doesn't say anything about genes: it only says that inheritance matters. Clearly, genes are the primary vehicle for passing on traits, but they're not the only way. And with humans, these other mechanisms are really important.

First, genes are not the only thing you get from your mother; they're not even the only thing in a mother's egg. If an egg only had DNA, it would be like... well, more like sperm.

There are other parts to these generative cells like the mitochondria, or the energy-producing part of the cell, which you only get from your mum. Researchers have realized that there's DNA in the mitochondria — 37 genes' worth — DNA that can give us important information about your mother, your mother's mother, and so on. But your mitochondria reproduce asexually from that egg cell, so you inherit your mitochondria only from her.

Research in the past few decades on the DNA in the human mitochondria or mtDNA has shown that we could use it as a 'molecular clock.' Because you only get mtDNA from your mum, and she from her mum, and so on, we can estimate how old a variant of mtDNA is by how many mutations have occurred. We can estimate, for example, how long ago two individuals shared a common ancestral form of mtDNA by comparing their mtDNA and estimating for how long it would take for all the intervening mutations to have arise.

Moreover, we've realized that Weismann's germ theory of inheritance wasn't entirely correct; some of your experience could leave a trace in your germ cells so that some kinds of change could be inherited, like the Dutch famine cohort passing on a pre-set stress response. The study of epigenetics, or the way that embryos form from fertilized eggs, helped us to see that the process was crucially shaped by DNA, of course, but also by other material in the mother's egg, and by processes that happened in utero or immediately after birth.

For example, a lot of the calibration of your immune system happens through breast-feeding, as your mother's milk affect how basic immune responses are sensitized to potential threats. And, as we've seen, starvation of your mother or other ancestor can prime your DNA to respond in distinctive ways, almost as if epigenetic processes were giving you a flying start to face the same types of challenges your ancestors faced.

In another example, if you stress out a mother, you can make her children shift their immune systems. The body uses inflammation to fight off bacterial infections, other immune system responses to fight off viruses. We're beginning to realize in research done on other primates — with data to suggest the same thing happens in human — that if you stress out a mother, her child's immune system will be tuned more to fighting bacterial infection, possibly arising from injury. In contrast, a happy, socially-engaged mum tends to produce a child whose immune system is better tuned to fighting viral infection, which you're more likely to get if mum is hanging out in a group with viruses circulating among them.

It's not all in your genes

Inheritance also takes more circuitous routes, however, not just through direct biological transfer. When you were born, you weren't simply tossed out a window with your genes and let to figure out things for yourselves. Like many species, you were cared for, defended, fed, and nurtured. You came into an environment that was already shaped by generation upon generation of humans who had come before you; otherwise, you'd have to be a lot more worried about predators, and there'd be a lot less built up around you.

Some evolutionary theorists have argued that one important way to think about non-genetic inheritance is to look at the way that many species, not just humans, alter their environment, changing it for future generations. They call it 'niche creation' or 'niche construction,' or the way that selective pressures faced by one generation are changed because of the actions of the previous generation. Not every species shapes its niche, but some change their environment a lot, for better or worse, so that you have to think about how accumulated activity alters the pressures that shape the species itself.

If the change to the environment is stable and persists over enough generations, it becomes both selective pressure as well as being a form of inheritance. The theory of niche creation is controversial; it make modeling evolution more complicated. If you take niche creation into account, you have to acknowledge that the environment isn't just driving an organism's evolution, but also being affected by that evolution. The influence can go both ways.

With some species, the impact is small. With others, however, the investment of in changing the environment is so huge, and the difference this change makes for the survival of the species so great, that it's impossible to ignore. For example, social insects like ants and termites produce large mounds, a combination of fortress and sophisticated breeding complex. The mound radically changes the survival rates of offspring and the traits of those offspring.

Beavers create artificial wetlands by building dams, providing for their own defense, multiplying the fish available to eat, and basically making an environment a kind of beaver water park. A young beaver inherits, not just genes, but a world altered to favour beavers; and their survival depends upon the interaction between their instincts and this beaver-created environment.

With humans, the niche creation dynamics are even more extensive and unpredictable. For example, our ancestors were really good at eliminating any animal that preyed on us, with just a few holdouts, like crocodiles and sharks, who are almost all in danger of extinction. Our ancestors' actions mean that you and I go about our daily lives without too much worry about attacks by bears or tigers or wolves.

Almost all forms of niche creation are unintentional, and some aren't favourable in the long run for the continued survival of a species. A species can change an environment to such a degree that the niche actually becomes inhospitable to itself or other forms of life. For example, many of the diseases that menace us today arise from our own domestic animals, or are exaggerated by the ways we alter the environment; malaria, for example, probably one of the selective pressure most affecting some pockets of humanity, is made worse because we cut down forests for fields, and then create breeding grounds for mosquitos in the stagnant water of irritation trenches.

Both epigenetic inheritance and niche creation are ways that acquired traits can, in some circumstances, be passed on. Maybe Lamarck wasn't totally wrong. Your experience can affect your offspring. But the most important way that this might happen is through learning and teaching.

Learning and teaching are the clearest and most crucial form of non-genetic inheritance. It's not just humans that learn: one of the most important reasons to have a brain at all, no matter how small, is to learn. And all kinds of species learn, even some of their most basic skills.

Song birds, for example, will start chirping as they develop as chicks, but they won't develop the adult songs that they need in order to reproduce unless they're exposed to adults singing. Their brains and senses are ready to learn, primed to pick up the right song. They're even instinctually experimenting with making sound. But unless they get the right environmental stimulus, they can't learn what they need to know.

The key difference with humans, then, is not so much learning, as it is *teaching*. All kinds of animals learn, but most have to do it for themselves. Although predators will sometimes give their offspring wounded prey to play with in order to learn, and others seem to show their young how to find food, humans build an elaborate social structure for teaching so that this channel can pass on an immense amount of the information that any human needs to survive.

Learning doesn't obey the strict inheritance patterns we find with genetics. In some species, yes, learning happens entirely from mother to offspring. For example, chimpanzees seem to learn foraging techniques and other social behaviours almost entirely from their mums. Because of the way that chimpanzees interact, it's hard to learn a skill from an unrelated adult or one of your peers. But it does happen occasionally.

In humans, however, lateral transmission — from peer to peer — and diagonal transmission — from an adult to another adult's child — happens all the time.

Sometimes, it's hard to draw a clear dividing line between learning and niche creation. For example, you learn language mostly without anyone trying to teach you. You don't sit down with a 6-month-old and say, 'Right, let's learn the words 'yes' and 'no.'' In fact, children learn to recognize their mothers' voices and their native speech sounds before they're even born, when their mother and other adults have no idea that the unborn child is listening in.

And humans are really good at teaching, even when they don't realize it. For example, most adults unconsciously shift the way that they talk to young children. They raise the pitch of their voices, simplify their language, and repeat themselves. If you didn't know better, you'd swear that they had lost it. Most adults have no idea that this is excellent teaching, structuring language so that it is easier to acquire.

We instinctually create a kind of cognitive niche, a cut-down-to-child-sized version of language and other activities that make it easier for a kid to pick them up: repetition, face-to-face, simplified, interactive. Most children are primed for this, geared up and receptive, with great social skills compared to other primates. And most parents are primed, too: sleep deprived, sure, but excited and ready to interact in ways that heighten how effective this channel of inheritance can be.

If a child has a problem with reception or social interaction — for example, gets too stressed out from face-to-face interaction or can't hear what's going on — or if the parent doesn't help to create a supportive niche — for example, if a mother has severe post-natal depression or people don't interact with the child — this form of inheritance can get undermined.

The good news, however, is that many of these developmental processes, these forms of inheritance, are really robust. Because they don't go strictly from parent to child, and they depend upon this whole human world we've built up, they've got all kinds of redundant channels.

The bottom line, however, from all these examples is that, if you want to understand us, humans, and why we're distinct, you have to realize that it's not all in our genes. Our genetic peculiarities create the possibility of these other mechanisms, which we can find in other species, but not necessarily to the same degree that we find in ourselves. The complete instructions to build a human aren't just written in our genes; we've also carved them into the world all around us.

Symbiosis & cooperation

Yet life is not all just competition. Our cells don't fight each other; colonies of ants and termites work together on a massive scale, even laying down their lives for the good of the nest; and primates and other animals lead complex social lives. Darwin recognized this and drew attention to the way that the animal kingdom was not simply vicious competition, but also involved dependence, inter-relations, even symbiosis.

Symbiosis occurs when two species live in close relationship and both derive benefit from that relationship. A parasite does not have a symbiotic relationship because the parasite, like a tick or a tapeworm, does not give any benefit back to its host. And both of these relationships are different to a predatory relationship because both require that the host remain alive in order to benefit. Symbiotic relationships can be quite close, or the links can be more indirect.

For example, we have a gut full of helpful bacteria that weigh more than our brain, more cells of bacteria than we have bodily cells because they're so small. That's right, you're a mobile home for 100 trillion microbes of hundreds of species — your microbiome. Without them, you'd survive, but it would be hard to digest everything you eat, and your immune system would suffer. That's a pretty tight symbiotic relationship — you and your (mostly) happy gut full of bacteria.

Other symbiotic relationships exist in the animal kingdom: ants and fungus that they farm, sea anemones and clownfish, cleaner fish and larger sea creatures, even bees and flowering plants. In all these cases, species co-evolve; that is, they become so adapted to the opportunities presented by the other, that one's evolution shapes the evolution of the other.

A more distant relationship is the link between living things through oxygen. Up until about 2.4 billion years ago, the atmosphere of our planet had much less oxygen. The rise of cyanobacteria, bacteria that could produce energy through photosynthesis, began to shift the composition of our atmosphere. Photosynthesis allows plants, algae and bacteria to create energy from light by combining water and carbon dioxide to produce a simple sugar, but it leaves loose oxygen as a waste product.

Over millions of years, the cyanobacteria created more and more oxygen; at first, this oxygen was mopped up by other geological processes, especially by oxidation, which we see as rust in iron compounds. But eventually, after 200 million years, the cyanobacteria filled these oxygen sinks, and the gas started to build up. In a sense, you can say that their pollution laid the foundation for the rise of complex life. In that sense, we are symbiotic with these organisms that can create energy from light because we literally depend upon their waste in order to breathe.

But this shift would have been a catastrophe at the time; all that oxygen wiped out the life that depended on that previous environment, and possibly contributed to a massive 300 million-year ice age. An ecological change was produced by a new form of life, laying the foundation for life as we know it in the mass destruction of what had existed before.

Cyanobacteria are also important to understanding the really important ways that novelty or variation can be introduced into species, through genetic sharing. Cyanobacteria are a key player in what the late biologist Lynn Margulis called 'endosymbiotic theory.' Margulis first began proposing the endosymbiotic theory in the 1960s against enormous opposition. She argued that complex, multicellular life was all the result of a form of symbiosis or inter-organism cooperation. According to Margulis, a single-celled organism engulfed its symbiotic partner; that's why we call it 'ENDO-symbiosis,' because one symbiot is inside the other.

Margulis took the work of earlier researchers who realized that parts of the process through which a complex multi-cellular organism reproduce — how one cell becomes two and so on — looked a lot like how bacteria reproduce. For example, the mitochondria in our cells, the parts that produce energy, and the chloroplasts in plant cells, the parts responsible for photosynthesis, go through their own reproduction process as the cell divides. Moreover, if you look closely at these little organelles, or parts of the cell, they have membranes around them like little Russian dolls, like they are compartments inside the cell. Margulis argued that complex eukaryotic cells, like the kind you and I have, were once cooperative little communities of independent parts that had grown together into a permanent endosymbiotic relationship.

Margulis went on to argue that the 'modern synthesis,' that combination of genetics with the theory of natural selection, had over-emphasized competition and mutation as the forces that drove evolution. Margulis described, instead, how complex life came about through cooperation, mutualism, and interdependence, especially through symbiogenesis, or the creation of new forms from the combination of pre-existing life, like the cyanobacteria being captured as on endosymbiot by another bacteria. Margulis argued that eukaryotic organisms — multicelled organisms — were the result of symbiotic microbes becoming permanently linked so that they required each other to live.

Margulis' theory, which had been suggested by Russian botanist Boris Kozo-Polyansky in the 1920s, took an enormous leap forward in the 1980s when the technology was developed to read the genetic material in cells. As Margulis' theory predicted, some parts of the cell, especially the energy producing organelle (the mitochondria) and the part responsible for photosynthesis in plant cells, turned out to have their own DNA, different to the nuclear DNA of the cell. Her theory was controversial at the time, and parts of it rightfully still are, but most biologists now accept that symbiogenesis is crucial to understanding complex multicellular life.

Like any radical thinker, Margulis may have over-stated her point, but symbiogenesis, even if it is rare, encourages us to look for other mechanisms, other than just mutation and competition, that might propel changes in life. Certainly, Darwin himself would have been interested in this kind of observation, for he had noted in *On the Origin of Species* how life grew in complex networks of inter-dependence.

Viruses & cooperation

One of the more controversial parts of Margulis' theory, the theory of endosymbiosis that we talked about in the last segment, was that variation in species wasn't just a result of incorrect DNA copies; rather, new genetic material might be introduced into the nucleus of a cell by either viruses or bacteria. Again, new research techniques have born out this controversial idea. We now realize that single-cell creatures can sometimes pass DNA laterally, that is, share amongst themselves, or even steal genetic material, rather than just get it from their parent and pass it to their offspring. This genetic sharing helps us to understand a whole series of evolutionary events, including even how sexual reproduction itself evolved, as we'll come back to next week.

But perhaps the most startling is the discovery of large amounts of viral DNA in the genomes of complex organisms, including our own. To understand how it got there, I have to explain a little bit about retroviruses.

A retrovirus is a little bit of RNA, the simpler single-sided cousin to DNA, that inserts itself into a living cell. The RNA then sort of reverses the usual order of things in the cell nucleus, by building a DNA version of itself and clipping that into the cell's DNA, using the cell's own reproductive mechanism to get itself copied. Some retroviruses are very dangerous to their host, for example, HIV and some that cause cancer.

But some less virulent of these retroviruses are so successful that they become endogenous. That is, like the endosymbiot, these viruses become permanently part of the organism's genome so that they get passed on to the organism's offspring. They manage to hack their way, not just into our body cells, or 'somatic cells,' but into our germline cells, the ones we use to make offspring, the ones that early twentieth century evolutionary geneticists thought could not be affected by anything that happened during an organism's lifetime.

In big, multi-celled animals like us, there's a lot of ancient retroviruses lying around, artifacts of previous attacks which our ancestors survived, or of insertions by retroviruses that weren't all that dangerous in the first place. In fact, researchers now estimate that there are about 100,000 pieces of viruses in human DNA, making up about 8% of all our genetic material, getting passed on from generation to generation. Some of them can still flare up into diseases; for example, endogenous retroviruses are now considered a potential source of auto-immune disorders, when the immune system starts to attack the body itself.

But some of this retroviral material gets used by the host in constructive ways, including to regulate gene activity. In fact, endogenous retroviruses are crucial for the formation of the placenta in all mammals. The placenta passes nutrients from the mother's body to the embryo, and it protects the embryo from the mother's immune system. Without the placenta, we'd have to still be laying eggs. The same mechanism that allows the retrovirus to latch onto a cell helps to fuse cells together in the placenta, so that mammals can essentially have an internal egg. If the ancestor of the mammals had not caught this retrovirus, we would still be laying eggs.

The point is not that this undermines the theory of natural selection. Retroviral insertions and endosymbiosis help us to understand that variation can arise in many ways and that 'selection' may mean fitness for cooperation, or the ability to find the right partner, not just competition. A living thing may find a niche to adapt to within the gut of another living thing, or even inside its cells. If this relationship helps the host, the addition may actually make that host more 'fit,' and more likely to reproduce.

In social life, we see this even more; selective pressures may favor living things that work well as a team.

Perhaps the most striking example of this is in 'eusocial' animals, that is, animals in which a substantial part of the population is sterile, like ants, termites and bees. Worker animals typically serve a queen; the majority of the species never reproduce. How could evolution favor individuals who cannot pass on their traits, for whom there is simply no inheritance?

We realize now that, for some species, 'inclusive fitness' is the key to understanding their behavior; 'inclusive fitness' recognizes that an individual's inheritance doesn't just come from its own offspring. Because you are closely related to your siblings, their children, too, can be seen as passing on a proportion of your genes. Inclusive fitness is one way to explain apparently altruistic behavior; saving your brother's or sister's kids means that you are creating more individuals related to you. Worker bees are an extreme example of that.

Another possibility is group selection. Building a stable, highly-integrated community may mean that your group is more cooperative; if resources are scarce, and communities have to fight for them, then tight internal cooperation might make your group prevail over rival groups. The idea of group selection leads some theorists to talk about multiple levels of selection; that selection acts on individual genes, on individual organisms, and on groups.

Both of these theories are themselves controversial, but no one disputes that cooperative behavior, even the rare but extreme form of eusociality, can be an evolutionarily successful strategy. The biomass of ants alone makes up more than half of all the insects on the planet.

Arguably, humans, too, have benefitted from cooperation. From a precarious, small population about 100,000 years ago, we have exploded in number, not just through competition, but also through an extreme form of cooperation. The total mass of humans on the planet is eight times greater than all wild vertebrates on land combined, and we have about the same mass as all the fish and whales in the sea.

Symbiosis with other species hasn't exactly worked out too badly for us either: our domestic animals outweigh all wild land animals by twenty times. Together, humans and their herds — all the pigs and cows and chickens and dogs — make up more than a quarter of all life on the planet by weight. We're even shaping each other's evolution, that is, co-evolving together.

We have gone from being a fragile, unusual ape to a world-changing organism in about 6000 generations, but this isn't the first time that a life form has worked this kind of massive change to the planet. You should know. You're breathing the evidence.

References and Resources

Key concepts

The basic theory of natural selection is that variation leads to difference in survival; if survival is based on traits that are well suited to selective challenges, and those traits are inherited, adaptation will occur over time.

The 'modern synthesis' combined Darwin's theory of natural selection with an understanding of genetics, especially a focus on population-level dynamics.

Our increasing understanding of genetics helps us to see the complexity of inheritance, including the possibility that gene expression may allow some experiential effects to be inherited.

Multi-cellular life and social organisms also involve some degree of cooperation, not just competition.

Resources

Darwin Online -- complete collection of manuscripts. (link)

Darwin exhibit (online) at the American Museum of Natural History. (link)

Interactive Voyage of the Beagle (online) at the Natural History Museum (UK). (link)

Ghost in Your Genes, NOVA, PBS (USA). Website supporting a special on epigenetics. (link)

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Sex

Natural selection is not simply about survival – an animal must also pass on its DNA. This creates the possibility of individuals competing with other members of the same
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species through reproduction. Our bodies offer us clues about how our ancestors reproduced, competed with each other, but also how they must have cooperated in order to reproduce successfully.

Sex: Why bother?

Why bother to have sex at all?

I know what some of you are thinking: 'You're obviously doing it wrong.' But I'm serious.

From an evolutionary perspective, lots of living things reproduce without sex. All single celled organisms can copy themselves. Even some very complex animals can reproduce asexually or by parthenogenesis. Some species of lizards, amphibians and fish, for instance, have no males; a female-only species simply lays eggs that are clones of themselves. Other species can reproduce either sexually or flying solo — such as the komodo dragon and hammerhead sharks — depending on the situation.

Although it might not sound like a lot of fun, from an evolutionary perspective, it seems like a win. After all, if you reproduce asexually, you pass on all of your genes to the next generation. If you reproduce sexually, you only pass on half of your genes; your DNA gets mixed with the DNA of the other parent, so a child is only half of you. If your genes were just being selfish, they wouldn't want in on that bargain.

In addition, sex limits your reproductive rate, slowing down the process, and it might even make it impossible to reproduce, if for example, you get eaten by a predator before you manage to find a mate. If you wash up on a desert island alone, you're not going to leave any offspring if you reproduce sexually. In contrast, an asexually reproducing animal might quickly fill the island.

Put simply: the cost of sex is males. If you reproduce asexually, you don't need them.

But sex has been around for over a billion years, so it must be good for something. We don't know for sure why sex first arose, but over time, sexual reproduction has accumulated a number of advantages, other than just having a good time.

The key is to understand that, from an evolutionary perspective, sexual reproduction is a trade-off: on the one hand, you limit your ability to reproduce. On the other hand, there are both genetic and ecological reasons why mixing together DNA from two parents, or recombination, might be an adaptive advantage.

First, and probably foremost, recombination produces a lot of variation, which as we know, is the raw material for evolution. Because of recombination, children are not clones of either parent, but are each new combinations of genes; each siblings is also different, even in cases of identical twins (although the differences are pretty slight).

Recombination allows traits that are beneficial to spread quickly through a population.

Even multiple traits can spread through a population as lines of inheritance cross and re-cross in a sexually-reproducing species, whereas reproduction by cloning asexually does not produce this crossing of genetic material. This pattern is so beneficial that some asexually reproducing single-celled organisms have come up with their own ways to do this, swapping genetic material from one to the next.

Recombination also can clean up genetic errors. Getting one copy of a gene from each parent may allow an offspring to overcome some copying errors. In an asexually reproducing species, you only get genetic material from a single parent; if it's defective, you're stuck with it, whereas with recombination, you are likely to have two copies of almost all your genes. For this reason, sex may decrease the possibility of extinction. Where we don't have recombination — like with the Y chromosome, because you only can get it from your father — we don't have this repair mechanism, and detrimental mutations can start to pile up. In a few million years, this is going to be a problem for us males of the species.

The advantage of sex, however, isn't simply that variation might produce a beneficial new trait or repair genetic damage. Sexual reproduction also makes a species a kind of moving target. All the time, other species are trying to figure us out. Viruses, bacteria, parasites —don't look behind you— they're all trying to crack your immune system, to find a way to break down your defenses. Sexual reproduction means that every individual is a new problem for the parasites and viruses to solve.

We call this the 'Red Queen' theory after the Red Queen of Wonderland in the book, Through the Looking Glass. Alice and the Red Queen were in a race, running as hard as they could, but apparently going nowhere. Alice, panting, says,

'Well, in our country,... you'd generally get to somewhere else — if you run very fast for a long time...'

The Queen responded: 'A slow sort of country!... Now, here, you see, it takes all the running you can do, to keep in the same place.'

Evolution is a bit like this race; it never stops, and you have to run as hard as you can to stay in place. Species that do not seem to change are undergoing constant selection, even if it is stabilizing selection.

A species like the horseshoe crab, apparently unchanged for millions of years and quite uniform one to the next, turns out to have a tremendous amount of genetic variation underlying its anatomical uniformity. Those species that reproduce by cloning may have their days numbers, as faster reproducing viruses are constantly generating new variants, one of which might be especially virulent, and parasites may load up on a stationary genetic target.

Sexual reproduction also produces its own evolutionary pressure: sexual selection. Sexual selection is an evolutionary pressure that is produced by intraspecific competition in order to mate: that is, animals must compete against members of the same species to mate, rather than against predators or the environment or some other external factor.

Consider the peacock, an animal that gave Darwin fits of anxiety until he figured out what was happening. A male peacock has an absurd tail. At the height of mating season, Mr. Peacock drags around an enormous, brightly coloured fan of these incredible feathers. They are so big that they make it harder to fly, so incandescent that they virtually announce the bird's presence to predators.

And if you've never been around them, male peacocks are even more absurd than they look: they shriek at the top of their lungs and do this wild shimmying dance whenever they see an eligible female peahen, or anything that vaguely reminds them of a peahen, including horses and dogs and sometimes their own reflections. Seriously. As the male peacocks dance back and forth and shimmy, they shake their enormous feather tails. It's all a bit much.

We now realize that they are engaged in a type of competitive sexual display; they are, in a sense, auditioning to mate with peahens. If a male doesn't have a terribly impressive tail, or doesn't put on the right show, he's not going to be fathering any baby peacocks. The female peahens exercise mate choice; if a trait is particularly attractive to the females, that trait will be selected in the males and tends to get steadily more and more exaggerated.

We know this because researchers have taken very successful males — peacock studs — and lopped off the bright eyes of some of their tail feathers. That mating season, with their reduced tails, the studs turned to duds, unable to impress with their paltry plumage.

Other male birds use their songs, build elaborate nests, or engage in ritualized dances to try to become the preferred choice of a female. This type of sexual competition is one way to make sure that a female gets the best possible mate; the healthiest, strongest males, theoretically, should put on the best displays.

Sexual competition

Peacock males and most birds don't compete face-to-face, but some species do engage in direct competition as a form of sexual selection. In bighorn sheep, for example, at the start of the mating season, or rut, rams have to sort out a dominance structure to determine who will mate. The male rams square off and literally go head-to-head, slamming into each other to demonstrate that they are the strongest. The dominant males tend to reproduce much more successfully, which can drive the evolution of the species.

In many primates, though not all, direct competition is also the rule. One of the most dramatic examples is gorillas. If a male gorilla is going to reproduce, he has to take control of a polygynous group of females. Polygyny is a reproductive system in which a single male mates with multiple females, but not the other way around. A male gorilla does this by deposing and taking the place of the male 'silverback,' the only male who can reproduce.

Among gorillas, only the strongest males pass on their genes to the next generation. The rest are effectively sterile from the point of view of evolution. This brutal sexual competition has produced extraordinary sexual dimorphism, or a difference between male and female forms of the same species. A female gorilla is big, but a male is enormous — a silverback is up to two and a half times the size of his mates. In addition, he has an outrageous skull, with terrifying canines and huge crests to anchor massive jaw muscles. The irony is that the owner of this skull is a vegetarian.

Direct sexual competition has driven gorilla evolution to produce an extraordinary set of weapons, all for the purpose of intraspecific competition, or fighting with other male gorillas. Over and over again we see this: sexual selection, intraspecific competition, can drive the production of more and more elaborate plumage, more extreme weapons, larger size in males, and a host of other phenomena that we call secondary sexual characteristics. We call them 'secondary' because, unlike primary sexual characteristics, they are not practically necessary in order to reproduce like testes and ovaries, although they are used in the behaviours that lead up to reproduction like courtship dancing or rutting.

Sexual selection tends to drive dimorphism, or create a marked difference in male and female form or behavior. In the elephant seal, for examples, the males — bulls — are six times larger than females.

In fact, the degree of difference between males and females, the degree of dimorphism, is sometimes seen as a good proxy measure of the intensity of sexual selection. The more intense the selection, the more sexually dimorphic a species will become, the differences becoming more and more pronounced. Males will develop bright colours, elaborate songs or dances, specialized weaponry, or greater size, which their female counterparts don't have.

But wait a minute, some of you may be thinking: why is it that males have to fight over females? After all, in Australia, we tend to read about supposed 'man droughts,' and we all know that women have to work hard to get a man, right? Beauty contests aren't held among men, are they?

Well, that's not what evolution and biology teach us.

To understand which sex is going to have to compete, we have to think about which sex does the most investing in offspring. The evolutionary theorist Robert Trivers, one of the most important evolutionary thinkers since Darwin, pointed out that in any species, sexual reproduction is a kind of joint investment of the parents. Trivers realized that, in most species, the parental investment of each sex is not equal.

For example, even in producing gametes, the gametes are not the same size: eggs and sperm are not identical. Over the last billion and a half years, one sex has tended to invest more heavily in each gamete, building a full mechanism to reproduce, a fully-fledged cell, around it; we call this sex the 'female' and this gamete the 'egg'. The other sex has tended to specialize in larger-scale mass production of little gametes, with little more than the DNA being transmitted, and spread them around. We call this sex, 'male,' and the job of 'sperm' is to get its half of the full complement of DNA to the 'egg,' where most of the equipment for producing life is waiting. The difference in gamete size is called anisogamy, and wherever you have it, you start to have sexual difference.

In some species, the females invest more in each offspring; in some species, it's the males. Whichever sex invests the most becomes a limiting factor on the reproductive rate of the species. Whoever has to sit on the eggs or look after the infants or carry them to term if pregnancy was long or feed them, is going to be a kind of brake on the reproductive rate of the species as a whole. Depending on how big the gap was, the other sex is likely going to have to compete more or less severely in order to reproduce.

In all mammals, females tend to be the limiting factor, unless the number of males has dropped off. That is, the rate of reproduction of a species is limited by the number of females in the population; because female mammals carry their infants to term, rather than simply laying a clutch of eggs and taking off, and because mammals feed maternally — it's how they got the name 'mammals' after all, because of the mammillary gland. So it's generally the females that engage in mate choice.

Trivers' hypothesis, that differential investment determines which sex will have to compete, predicts that human males will have to compete to mate, not females. You would never know this if you listened to Western popular culture, of course; you would assume that women have to try their hardest to attract a male, but that's not at all what evolution suggests.

Like virtually everything with humans, we make things more complicated than they are. Sex is certainly no exception.

Males and females

Our popular culture wants us to believe that men and women are fundamentally different, even opposed: men are from Mars; women are from Venus. Boys are made of snips and snails and puppy dog tails; girls, from sugar and spice and everything nice. Pink and blue. Opposites attract. All that sort of thing.

In fact, we are not so different. Women and men are both from earth, not Venus or Mars. And if we have a lot in common with other species, we have even more in common with each other. We may have ideas about gender, what is masculine and what is feminine, built up in our culture, but our biology tells a slightly different story.

First, male and female bodies are fashioned in the same workshop, tweeks on the same basic design with a raft of surprising homologies at the same time that there are also some really important differences. We've got to remember this, even when we read research about the evolution of human sex and reproduction because too often, this research starts from our cultural attitudes or folk assumptions about the supposed gulf between men and women.

Students are sometimes startled when we point this out anatomically. For example, the testes and the ovaries begin life as the same organ, the scrotum starts out as the same tissue as a labia, and we all have the same basic hormones, just in different proportion. If you listened to popular culture, you'd think testosterone was a kind of 'boy juice' and estrogen makes you female. In fact, women have testosterone, just as men naturally have estrogen. Sure, levels are different in both, but take away either of these hormones from men or women, and you'll get health problems.

The point is that, although we tend to focus on and even exaggerate the differences — and I'm going to discuss them, too — male and female are homologous. In fact, up until about six or seven weeks in utero, you can't tell whether a child is male or female from its gross anatomy; you have to look at its chromosomes because the differentiation processes haven't kicked in yet. An embryo starts off as anatomically indeterminate.

All that changes in week six, when, in the case of boys, masculinization starts. On the Y chromosome, present only in males, a gene imaginatively called the 'Sex-determining region of the Y chromosome,' or SRY, up-regulates certain developmental processes in a kind of chain reaction that leads to testes formation. Cells responsible for a spike in testosterone appear in the testes, which are still up inside the abdomen at this point, and they start to pump out extra testosterone in week eight. Production doesn't peak until around week twelve of uterine development. The penis and male gonads will mature until around week fourteen, you get the first sperm starting to form. It becomes possible to tell externally that an embryo is male as early as the third month of development.

Women's bodies start off a bit slower, but catch up quickly. About week eight and nine, the vagina and uterus form if the embryo does not have that gene, SRY. The first ovarian follicles, which will become eggs, appear around four months of development. If, for some reason, the embryo is insensitive to hormonal effects, for example, does not have receptors for the hormones that bring about masculinization, the default outcome looks female, but will not be able to reproduce if it doesn't go through the feminization process. From this perspective, 'female' is sort of the default state for the embryo.

Every once in a while, a child is born with indeterminate sex; some of the more conservative estimates suggest that the number is between 1-in-500 and 1-in-2000. Although quite rare, what these individuals help us to recognize is that sex is not a switch that's flipped either to male or female. Sexualization is a biological process and, in some cases, doesn't go on to produce either male or female.

As part of this process, many of the secondary sexual characteristics don't show up until puberty, starting around age 10 to 12; at puberty, another round of hormonal changes propels sexual maturation. A spike in estradiol in girls cause the breasts to enlarge, body shape and genitalia to change, and menstruation to start, the onset of adult fertility. High androgen production in boys at puberty brings about a host of changes, including to the sex organs, voice, body hair, overall build, and behavior.

Even after we mature, although we may believe that male and female are quite different, our sexual organs behave in quite similar fashion, revealing the underlying homology. When we're sexually aroused, for example, blood rushes to the homologous organs — the penis and the clitoris — causing swelling and flush, and the metabolic processes are virtually identical in terms of heart rate and patterns of excitation.

There are important differences, of course. Men are, on average, larger than women, have greater upper body strength, and seem to have a higher metabolic rate; women appear to be better able to fight infection, mature younger, seem to be better at laying on body fat, and, of course, lactate and menstruate.

A lot of evolutionary theorists say that, if you compare us to other primates, we're a bit more dimorphic than the purely monogamous species, but much less dimorphic than the polygynous primates, like gorillas or orangutans. From the slight difference you might predict a slight tendency toward polygyny, or a tendency for males to have more than one mate.

In fact, for the past three or so million years, our ancestors have probably been staying the same or, possibly, getting less dimorphic, closer to equal. If our ancestors were more dimorphic — and that's a topic of some debate — then female hominins have been getting larger faster, so that they're about 80 to 85% caught up. That may not mean that we've been evolving gender equality, but it does suggest that, if males are competing, they're not doing so directly. If males were engaged in sexual competition, we'd expect that some clearer sign of that competition from the past few million years.

In contrast, if we look at our most closely related cousins, studying the trajectory some of the other great apes have gone through over the last ten or twelve million years, we see that our species does not have the hallmarks of strong male competition.

Bodies don't lie

Just like our bodies offer details of past selective pressure, they also have clues of the ways in which our ancestors reproduced, especially if we compare ourselves to other species. Let's start with what men's bodies tell us to try to get some clues about the evolutionary pressures on our ancestors from sex selection.

First, male gorillas have really small testicles and low sperm counts. No one really brings it up around them because they're these mountains of hairy muscle, but they've got pretty unimpressive balls.

In contrast, male chimpanzees have comparatively large testicles and high sperm counts. Even though the male chimp is about a quarter of the weight of a gorilla, his testicles are four times larger than his over-sized distant cousin. These disproportionately large testicles allow a chimp to have sex multiple times a day without sperm count dropping off too badly, possibly four or five times. (Of course, the chimp isn't all that impressive when you realize that a lion can mate 75 times a day during the mating season.)

Why the difference between chimps' and gorillas' testicles? Because male chimps engage in a form of sexual selection called 'sperm competition'. When a female chimp is fertile, she mates with a number of males. The dominant male in the troupe may try to keep other males away, but it's mostly a lost cause. Primatologist Jane Goodall observed one female chimp mate 84 times with seven different males in her troop over eight days when she was fertile. In a sense, each male's chance at fathering a child is sort of like an evolutionary raffle, with more sperm acting like more tickets in the raffle. We'll come back to why when we discuss women's bodies and children in the next video clip.

Chimpanzee males have faced so much to sperm competition that a large portion of their sperm appear to be suited, not so much to impregnate a female, but more to block or chemically kill sperm from other males. Some biologists suggest that as much as 99% of chimp sperm is not there to impregnate a female, but is better designed for sperm warfare.

Another way to look at it is that, gorilla males settle who is fittest directly, by fighting violently to monopolize sex. In contrast, chimpanzee females mate with a bunch of males and let their sperm sort it out. Since the last time that chimpanzees and gorillas shared a common ancestor, the two have been under these radically different pressures of sexual selection.

Human males don't look like either chimps or chimpanzees, and some of the data is controversial, to say the least. On the one hand, we've got nowhere near the testicular endowment of a chimpanzee.

On the other, men's bodies seem to anticipate the possibility that a partner has mated with someone else, unlike the gorilla. In fact, the amount of sperm that a man ejaculates is correlated, not with how long it has been since he last had sex, but rather with how long he's been apart from the women with whom he's mating. If they've been apart for a while, he can up to triple the sperm he would normally pass on. The male body seems to anticipate the possibility that a partner has had sex with another male and responds by upping the ante, a clear sign of adaptation to sperm competition.

On the other hand (yes, that's at least three hands...), human males aren't that well endowed with testicles. After the first ejaculation of the day, sperm count drops off precipitously; you can have another go if you like, but you're no chimp. More than 3.5 times a week, and your sperm count will suffer. In other words, our cultural ideas about males may suggest that they want to sow their wild oats: evidence from our bodies is that men may not have a whole lot of extra oats to sow.

But an even more interesting little comparative detail that may tell us about sex selection is penis size. Male gorillas, on average, have erect penises that are about 3 centimeters in length, or about an inch and a half. In contrast, the much smaller male chimpanzee has an average erect penis length of around 8 cm. Humans usually come in around 13 cm (according to scientists, not to the men themselves), disproportionately long and thick for a primate.

Moreover, the human penis is unusual, with no penile bone to keep it erect — other primates have an actual bone — men instead use a complicated hydraulic system. Although it might be for sperm competition, some sex researchers point to the unusually large, thick and hydraulic powered penis as a potential target for female preference, an example of how women's mate choice may have affected our hominin ancestors.

If we turn to the evidence from men's bodies, then, we find clues about our ancestors' mating behavior, but not necessarily what some people might think. Back in 1967, zoologist Desmond Morris, the author of *The Naked Ape*, could confidently write that the evolutionary purpose of human sexuality was 'to strengthen the pair-bond and maintain the family unit.' Man, has that confidence taken a beating!

The truth is, genetics has delivered another blow to some of our more romantic ideas about monogamy or 'mating for life,' even in other species that we thought were models of fidelity. Genetic testing in the field with wild animals has revealed that even some species that we thought were thoroughly committed often have high cuckoldry rates. That is, the chicks or pups or whatever turn out not to belong to the fellow who is hanging around most diligently. Gibbons, for example, once held up as the model of a monogamous great ape, turn out to be more wide ranging, the females especially engaging in extra-pair couplings when they are most fertile.

Some researchers have controversially argued that evidence suggests human females may have adapted to a pattern of seeking long-term support from a male partner but occasionally getting genetic material from a different male. Or, as the scientists euphemistically put it, they have a partner but, especially when they're fertile, may engage in 'extra-pair coupling.' (If you're still not with me, that means they're sleeping around.)

Supporters of this theory have pointed to genetic evidence in Western countries that many children have the wrong man listed on their birth certificate as their father. This is hard research to do, but it's well known in medical circles that a range of tests for things like the inheritance of disease typically uncovers that somewhere between 5 and 10% of the population in countries like the US and the UK and Australia could not possibly be related to the father listed on their birth certificates.

Even female orgasm may be a mechanism for a woman to, inadvertently, give the sperm of a preferred partner a greater chance of impregnating her. If so, this mechanism assumes that a woman is mating with multiple partners.

The point is that, when we look more clearly at the evidence our bodies present, and compare ourselves to those species to whom we're most closely related, we may find that evolutionary dynamics do not necessarily confirm our assumptions about the nature of men and women. The pressures of sexual selection have left traces upon our bodies, but they do not determine how we must act.

How our babies made us

When a horse is born, it's almost ready to stand up. Within an hour, the foal is on its feet. By the end of the first week, the baby's running. Awkward, sure, but you try to catch one.

We say that a horse is a precocial infant. 'Precocious': quick to develop. Its mum looks after it and will nurse it, but the newly born horse is quickly able to do some of its most important tasks for itself.

In contrast, check out a human infant at birth. Yeah, cute, magical and all that. But totally helpless, and it stays that way for a long, long time. Can't feed itself. Can't walk. Can't go out and hunt, clean itself, dress.... Nothing. Dependent upon its parents until it's what? Five? Ten? Twenty-two?

No, seriously. Studies of hunters and gatherers reveal that a child will finally produce as many calories as it consumes when it reaches no less than about 18 years of age in many foraging groups. Up until then, it must depend on others for at least part of its nutritional intake. One anthropologist has estimated that it takes *13 million calories* to get a child to a point where it can support itself.

This is an extraordinary ask. In most species, as soon as they're weaned, animals can provision themselves. In other great apes, for example, mothers nurse young for a long time, sometimes longer than humans, but weaning means independence. You're out on your own, and the next sibling is there to take your place.

Not in humans. Getting food is so information dependent in foraging groups, and children so immature relative to adult tasks, that it takes a lengthy apprenticeship to be able to take care of yourself. So the children start to overlap, one being born before her or his predecessor is independent. Orangutans can wait for a child to become nutritionally self-sufficient to have another baby — it takes them about eight years between births — but in humans, we can't wait that long. We'd only be able to have a child every decade-and-a-half or so. Our fertility is already low; that would probably drive us to extinction.

This patterns marks humans as extremely altricial. They require extensive care and support for a long time.

We don't really know for sure why we give birth to such immature infants; we used to be quite confident that it was because of the clash between the growing size of the infant's head and the mother's narrow pelvis, adapted to bipedalism. Anthropologists called that the 'obstetrical dilemma,' a conflict between the biomechanics of walking and the ability to deliver a large-brained infant if you carried it for too long.

Now, it's becoming clearer that the obstetrical dilemma isn't as bad as we thought; it would be possible to grow a wider pelvis if that was really the issue. Instead, the issue appears to be that this big-brained infant is an energy sponge in utero, creating a metabolic crisis as it grows and grows. In a sense, we have to have our infants when we do, even though they're so helpless, because they've hit a metabolic ceiling; any larger, especially with their growing brains, and there just wouldn't be enough nutrients in the system. What we've got to realize, and we'll come back to it next week, is that brains are expensive in energetic terms; they gobble up calories at a high rate. The mother can't keep up and must eject the child, where it will be possible to keep up with its voracious appetite.

You may not have thought of it this way if you haven't had a child of your own, but there's actually a deep conflict between mother and child. The demands of our children have shaped, not just mothers' bodies, but the whole of our species, during evolution. Although evolutionary stories about the origin of humanity used to focus almost *exclusively* on men’s business — hunting, fighting, finding a woman to mate with — feminist criticism and better science have really turned the spotlight on women and infants in the past few decades.

If you had asked an evolutionary theorist forty or fifty years ago, for example, about the forces shaping women’s bodies, *he* — most of them were men — would probably have said something about attracting men or hanging onto a mate. Recent research on sexual selection, however, turned that on its head. If we can see traces of our *female* ancestors’ preferences in men’s bodies, we can see the imprint of our *infants’* demands on women’s bodies.

For example, one of the most obvious distinguishing secondary sex traits of women is a higher body fat percentage than men and a distinctive body shape, with that fat deposited on the breasts and hips. Human women, for example, have fatty breasts. No, I’m not talking about just some women: all human women. You don’t need that fat to produce milk; other primates produce milk without fatty tissue on the chest, no problem. Same thing with the hips and buttocks. Again, unusual, compared to other species, and apparently unnecessary.

Trivers’ explanation of sexual selection has taught us that this extra fat on breast and hips likely isn’t there to attract males. The cross-cultural evidence supports this hunch: men in some societies may find one of these part parts erotic, but others don’t. We realize that males would be more likely affected by mate choice, not doing the choosing.

Increasingly, we think that the fatty deposits have more to do with infants’ hunger than with potential mates’ desire. The extra tissue may be a kind of insurance policy against low-level starvation that could interfere with a mother lactating. Our ancestors lived by foraging, and food may not have always been easy to find. They probably had to survive some pretty lean periods. An infant’s brain is growing so fast after it is born, at rates only seen in utero in other species, that the infant needs constant top ups of energy. Extra fat storage could be one way to make sure that you don’t get a temporary milk shortage, which could have a devastating impact on brain development.

Similarly, human infants are born disproportionately fat, as well. Other mammal infants aren’t born such little chunks. Sarah Hrdy argues that the baby fat is not just there to consume, but advertises to the mother, ‘Hey, I’m a very healthy, strong, cute baby. You should invest your energy in me!’ Hrdy points out that, because the interests of infant and mother do not perfectly coincide, and because human mothers have to make tough choices about how to allocate scarce resources, a baby has to persuade its mother to fulfill this challenging role as provider.

This conflict between an energy-hungry child and its mother, then, is part of a greater pattern in human reproduction. The mother-infant relationship is the social centre of all primates’ universes, but this centre is not harmonious. A mother’s and an infant’s interests, from an evolutionary perspective, do not perfectly coincide.

First, it’s in the infant’s interest to survive at all costs, regardless of the consequences to the mother, to get as much nutrition as it can in embryo, for example, and be born as large and healthy as possible. Babies want it all.

For a mother, passing on her genes may involve trade-offs, cutting losses with an embryo that isn't optimal, and limiting her contribution to one offspring so as to support a number of them. A mother wants to ration herself in the face of an infant's demands because her evolutionary legacy is not a single child, but all her children, including ones potentially not yet born.

Part of what makes this difficult to see in Western societies and other wealthy groups is that infant morality has been significantly reduced there, and fertility often quite low per woman, even though our calorie-rich diets make modern women capable of having babies very quickly.

For much of our existence as a species high infant mortality would have been an important evolutionary pressure. Our fertility isn't very high compared to other species, and it would have been a lot higher before the advent of birth control, but prior to agriculture, mothers probably wouldn't have been able to have a baby but every five or so years. In some foraging groups still alive today, mortality of infants is so high, and fertility sufficiently low, that some women leave no descendants, even though they may give birth to a number of children.

Struggles with children

From an evolutionary perspective, having a baby is not the goal — getting that baby to survive until you have grandchildren, preferably a *lot* of grandchildren, is. The problem is how altricial our infants are. Recruiting help to keep a baby alive, and sometimes making hard choices about how to allocate your resources, have probably been important to our ancestors for a very long time.

One example of how a mother's body, without her knowledge, makes tough choices, resists a baby's demands, and weighs the viability a fetus is menstruation. Menstruation happens because a woman, when she's fertile, builds a uterine lining during her cycle and then expels part of it after her peak of fertility passes. Many mammals do not menstruate; instead of building a uterine lining and then expelling part, they wait and only build one if there's a fertilized egg. Or, if they build the lining, they reabsorb it if it's not used. You don't have to menstruate to reproduce.

We now realize that there are at least two good reasons to menstruate. First, menstruation may be a kind of stress test which can expel embryos that are not sufficiently embedded to be viable over a whole pregnancy. Menstruation checks a pregnancy very early to see if it's worth investing in, or if the process should just be started over. We know that a lot of conceptions get naturally aborted early on; around 30% of fertilized eggs are expelled in the first few weeks, with as many as 50% of all conceptions terminated early naturally.

The second reason women may menstruate is that they have to build a uterine lining in advance to be ready when that energy hungry fertilized egg implants, so that the mother's body can resist it getting too deeply embedded, too hot-wired into her system.

Evolutionary biologist David Haig, originally from Australia, but now teaching at Harvard, has pointed out that many of the complications of pregnancy may arise from a silent struggle between the mother and the fetus. Haig argues that the placenta, once it forms at the end of the first trimester, is under the control of the fetus. The placenta actually invades the mother's tissue and reroutes as much blood as possible by restructuring the mother's arteries so that more blood flows to it. At this point, the mother can't control the flow of nutrients to the fetus without cutting the nutrients in her own blood, and the placenta can release hormones directly into the mother's blood to try to wring out more nutrition.

The fetus and the mother get in a kind of 'food fight,' battling after each meal for more of the glucose in the mother's blood. The mother's body tries to absorb it quickly; the placenta releases hormones to try to stymy the mother's ability to rob it of glucose so that more winds up with the baby.

In some cases, this struggle can produce gestational diabetes in the mother. Although we now think of this as a health problem, the condition leads to a particularly fat, healthy baby, especially in an environment where obesity is not a danger. Gestational diabetes is a sign that the fetus and placenta are getting the upper hand, undermining the mother's ability to produce insulin, which would keep that blood sugar down.

Once the baby is born, it's still terribly demanding, so much so that it can undermine a mother's ability to reproduce as much as possible. Unless she can get a break, she's not going to be able to have another child for a while.

One of the ways that human mothers respond to this demand is, unlike other primates, they recruit a lot of help to raise children. Anthropologist Sarah Hrdy has pointed out that most primate mothers jealously guard their offspring, and their offspring cling to them constantly until they're weaned, when a younger sibling takes their place. Humans are part of a rare subset that shares childcare, handing off infants to others, even nursing the infants of other mothers.

The pattern is alloparenting, or cooperative parenting by someone other than the two biological parents; in humans across cultures, this includes especially, grandparents, the mother's sisters, and even the child's older siblings. Hrdy says that to raise a human with a human brain takes more than a mother; in a sense, we evolved to need more than the usual primate single parent.

Hrdy's research on primate childcare has helped us to see just how strategic reproduction can be. She was the first to recognize in primates, that if a new male became dominant in a group, he would kill all of the children of his deposed rival. The reason is that infanticides brought all the mothers into fertility again. Hrdy also realized that females had strategies of their own, such as mating with multiple males to confuse them about which was the father; that way, a change in the dominant male was less likely to infanticide.

Being a mother was just as strategic as fathering children, Hrdy explained. For example, she argued that motherhood was not dominated by a 'maternal instinct' but could be much more strategic, involving a critical tradeoff between quantity of offspring and quality of investment in each one.

Hrdy wasn't the first to argue that our infants' needs were so great that it required cooperative parenting, but she made it clear that this didn't necessarily mean the father had to stick around, even though humans had evolved as cooperative breeders. Human parenting could recruit sisters, grandmothers and even the child's siblings. This research undermined the idea that the 'nuclear family' — mother and father with children only — was the natural evolutionary unit. The evidence was clear, not just from other primates, but from a lot of non-Western societies, that childcare was often much more widely distributed.

Hrdy's theory of alloparenting also explained the strange, extended survival of grandmothers, long after menopause, when you wouldn't think that their survival would matter evolutionarily. In humans, staying alive to be a grandmother meant you could pitch in to help make sure your genes survived in your grandchildren.

The bottom line is that we now realize that babies are not just packets of DNA. They are an investment of parents, have their own evolutionary strategies for trying to stay alive, and shape adults to a degree we may not have realized. Although many people *believe* that unconditional maternal love is a kind of natural instinct, biological observations, including comparisons with other species, remind us that reproduction is not so simple.

Long, slow sexual revolution

In 1672, after his brother fell off a horse and died, Moulay Ismail ibn Sharif became the Sultan of Morocco. He was an extraordinarily ambitious man: under his rule, Morocco conquered its neighbors, grew to an empire, fought off the Ottomans, and went through a building spree to try to make the capital, Meknes, a rival to Versailles. Ibn Sharif also had a prodigious capacity for cruelty: he legendarily ordered that the walls of Meknes be decorated with the heads of 10,000 enemy soldiers.

But history will likely most remember Ibn Sharif because he fathered more than a thousand children. There's no definitive count because a European visitor recorded 867 in 1703, but Ibn Sharif was barely two-thirds through his reproductive campaign. He kept at it for another *18 years*. According to one estimate, he had sex twice a day, every day, for his sixty-year reign, collecting approximately *4000* wives and concubines.

In contrast, history does not even record the name of the woman who gave birth to the record for the most children; we know her only as the wife of Russian, Feodor Vassilyev. During her lifetime, Mrs. Vassilyev gave birth to *67 children*, including 16 sets of twins, 7 sets of triplets, and 4 sets of quadruplets.

From Ibn Sharif's selfish perspective, his approach to reproducing might make sense; you might even think that evolution programmed Ibn Sharif to want as many children as possible. But if you look at it from the point of view of the species as a whole, Mrs. Vassilyev is more interesting.

Because, *if* Ibn Sharif had 4000 wives and concubines, and anything less than 2000 children, the fertility rate of women in Ibn Sharif's harem —assuming that they didn't have other children— was more than *130 times lower* than Mrs. Vassilyev. Tremendous reproductive capacity got *wasted* in the palaces of Ibn Sharif. A population of Mrs. Vassilyevs would have quickly swamped a population of Ibn Sharifs, outproducing them spectacularly, *if* the behavior pattern was inherited (and I'm not saying that it was, or is). The point is this: from an evolutionary perspective, what might make sense for an individual may not make sense for the good of a species.

But the other thing to notice is that, in both cases — Mrs. Vassilyev and Ibn Sharif — their incredible fertility was not merely the result of desire or genetic selfishness, but of the human capacity to cooperate and organise. Ibn Sharif attained his reproductive success, not because of unbridled natural instinct and selfishness alone, but because of quite sophisticated social and logistical tools: religion, government, military organization, trade, large-scale networks. Likewise, Mrs. Vassilyev could only have been so fertile given agriculture and a sedentary lifestyle. I daresay she probably didn't raise all 67 children by herself.

Both of them owe their fertility, not just to good genes, or to well-functioning reproductive systems, but also to the extraordinary social skills of humans. They both underline that reproduction isn't a solo operation, or even just a partnership; it's a collective project for humans that has shaped us.

Sometime in the past five million years, humans went through a profound sexual revolution, a shift in reproductive strategies that didn't just change how we had children, but made it possible to build this unprecedented human way of life.

Our current situation can make it hard to perceive the reproductive pressures our ancestors faced. Like Ibn Sharif and Mrs. Vassilyev, we live with the social, cognitive, and technological benefits that were won, in part, by this ancient reproductive revolution, just like we live on a planet crowded by our reproductive success.

Today, if we think about human population at all, many of us worry about *high* rates of reproduction, about the enormous number of us. But we, humans, were once small in number, and may have nearly died out at one point. Our fertility was likely low — compared to today — infant mortality high, and life hard; we had to cooperate to survive. The success of our species has been won by such unusual social abilities that one of us can even engage in the incredibly anti-social behavior of someone like Ibn Sharif.

Anthropologist Sarah Hrdy argues that cooperative breeding and alloparenting were key to our ancestors' success. Cooperative breeding means that a mother alone is not responsible for raising an infant; other people, including perhaps her mate, a child's grandmother, aunties, other adults, even older siblings — what Hrdy calls 'alloparents' or 'other parents' — helped to raise the child.

According to Hrdy, cooperative breeding and alloparenting didn't just feed babies and keep them safe. Cooperative breeding produced a human who was emotionally modern long before we had anything like modern technology, probably even before our ancestors developed sophisticated forms of cognition. We weren't simply social like other apes; we were 'hyper-social,' overly empathetic, seeking approval from each other, cooperative even when we must sacrifice for it... Basically, compared to other apes, we're huge suck-ups. How could evolution produce such a bizarre, 'please-like-me' ape?

Hrdy thinks that our pro-social nature is shaped by mating, in more ways than one. We're made more social, not just by the way we reproduce, but by the difficulties of raising a child, and being a child, trying to make sure the adults keep us alive.

Take, for example, our intelligence. In cognitive tests, chimpanzees, orangutans, and human infants score quite close to each other in remembering where things are and the basic way that objects work in the world; apes, including us, are good at problem solving such as figuring out cause and effect.

However, human infants are *much* better at social cognition. Human infants read others' intentions better, figure out what people are thinking, and notice social cues like pointing much better than other apes. Cognitive theorists call this 'theory of mind' but we might just call it 'social savvy.' We seem to be primed to interact, even to manipulate and deceive. Moreover, we create environments for our children where these skills are nurtured; we interact with babies, play with them, talk to them and share with them, just as we share them with other adults.

Getting passed around among different caregivers likely affected our intelligence. Most great apes cling to their mothers until they're weaned. Our ancestors likely got passed from one adult or older sibling to the next, developing a rich social world and sensory experiences. Instead of learning only from their mothers, out ancestors might interact with and observe other adults. Cooperative parenting produced new lines of inheritance just as it produced a hungry sponge of an infant.

Given this environment, infants' social skills also improved: being a cute baby had a survival payoff. Being able to read your caregivers emotionally and respond to them to get what you wanted would have been a huge advantage.

Even things that may annoy us might have their roots in this social environment of shared care. For example, some of our nearest ancestors, bonobos or what are sometimes called 'pygmy chimpanzees', don't really cry; they just sort of whimper. It makes sense. Producing a lot of noise if you live in a forest with predators can be a terrible survival strategy. Besides, if you're a bonobo infant, you're basically hanging on your mother, anyway, so you don't have to cry very loudly.

In contrast, our children can go off like a car alarm, sometimes crying for minimal reason; that's a great strategy if you're fighting for attention in a group, or maybe need to remind your older sibling to pay more attention to you. According to Hrdy, human infants got better and better at manipulating their carers, provoking our sympathy — they were now in competition with each other for attention and support.

Confusion, with benefits

Getting help with childcare, passing your baby around, would not have been possible unless a mother had a lot of confidence in the other people around her. If rival females might kill an infant, or disinterested males neglect it, this kind of childcare wouldn't be possible.

Our nearest relatives are not as socially cooperative as we are; chimpanzees have trouble sharing food, even with their *own* offspring. Other monkeys who cooperatively parent like humans, however, are similarly generous. Certainly, humans living together as foragers share food, even with children who are unrelated to them, and even in times of hardship.

Cooperative parenting allowed our children to grow up more slowly, taking the pressure off us to mature as quickly as possible or risk dying before we had a chance to pass on our genes. The cooperation also meant our mothers didn't have to delay going back into reproduction. The window of development, when the brain was immature, started to grow wider still, with consequences we'll talk about next week.

Without a change in the way that they reproduced, our ancestors wouldn't have developed more advanced technology, larger and larger social groups, and our distinctly human way of life. Our ancestors didn't know what they were doing — this sexual revolution was long and slow, so long and slow that our ancestors couldn't have observed it — but we inherit the legacy of this sexual revolution, including a set of important confusions.

One of the most productive confusions is that we don't know when women are fertile.

I live with horses, and nothing could be clearer to them as when a mare is fertile. During their reproductive season, when they're in heat, all hell breaks loose. The stallions get excited. Even the *geldings* get fired up, and they've got nothing to work with.

And, if one of them, stallion or gelding, manages to get anywhere close to a mare who's peaking, she will spray a pheromone-saturated fountain of urine in his direction, driving him into a froth. The mares will sometimes even do it to each other, probably because we keep them away from the stallions. If you actually let a stallion into a paddock with a mare in heat, complete chaos: nothing else will matter to either of them except sorting out whether or not they will mate.

Many animals are like this. Mating is a compulsory affair, even a kind of collective temporary insanity.

In contrast, human females are pretty damn subtle and under-stated. We don't know, without testing, when a woman is ovulating and most likely to conceive. We may notice some subtle changes in women's behavior, and the behavior of those around them, when women are at their peek of fertility — we tend to get more flirty and think each other is more attractive — but this isn't conscious. Perhaps the most interesting thing about humans is the degree to which we're kind of oblivious to this really important basic fact of reproduction.

We go through our daily activities unaware of whether the woman at the table next to us in the cafe is reproductively primed or in an off-peak period, so to speak. I can teach a classroom full of university students without anyone signaling that they have an egg ready to fertilize.

As a species, human women have ‘concealed estrus’; they hide almost entirely their fertility. We’re not the only species that does this, but we conceal it to such a high degree, especially given our intelligence, that we have to wonder how this is adaptive or at least not maladaptive.

First, it’s obvious that human women don’t need to signal estrus to get men interested in them. Whereas males of other species can be pretty ambivalent about females, or anyone’s company in general, without the right pheromones, human males don’t have too much trouble getting in the mood even without chemical encouragement. Same thing for human women, too, of course; they don’t have to be drunk on their own hormonal processes to mate, and will even mate when they are not fertile.

This kind of readiness for sex, even when unlikely to result in pregnancy, could have provided a social glue for increased pair bonding. If men didn’t know when their mates were fertile, then mating repeatedly might have been a more successful reproductive strategy. Males also might have stuck around closely with females in order to try to make sure that they didn’t mate with a competitor when fertile. If that male was willing to help with cooperative parenting, all the better, but it wasn’t necessary as a mother had alloparents.

Second, estrus has a cost: signaling fertility can be metabolically demanding. The most obvious examples are female primates who develop extremely swollen, red buttocks during estrus. This signal catches the males’ attention, but it sure takes metabolic energy, makes mobility more difficult, and may even expose the animal to danger of infection or injury.

Third, concealing estrus might have made it possible to conceal too the paternity of a child. As Sarah Hrdy found with other primates, males are reluctant to mistreat children that might be their own. If females were promiscuous, and males didn’t know when they were fertile, it might prevent infanticide; a guy wouldn’t kill an infant if he thought he might be the daddy.

Concealing estrus, however, may have more wide-ranging implications for humans socially. In some species, estrus can be a rough time: sexual competition intensifies, males fight to mate, and they may bully or isolate females in order to try to prevent mating with other males. It’s not just that the lady next to you has swollen buttocks or is pumping out pheromones; it’s what those signals do to everyone else in your group.

In contrast, humans can gather in large numbers without anyone trying to mate with the ovulating females — well, you know what I mean. You have no idea in a group who’s fertile, so, if you’re male, you wouldn’t know who to fight for, even if you were so inclined.

We can tell from the changes in our ancestors that the pressures of sexual selection did not favor males built for fighting — as in gorillas — or males built for promiscuity — as in chimpanzees. In fact, the steady or decreasing dimorphism in hominins over the last two or three million years suggests that direct competition hasn't been a strong force on our development. Instead, there's strong evidence that our fragile, needy babies helped us to learn to cooperate. And the way we took care of them drove their social intelligence and skills to unprecedented levels.

Our babies helped to make us human.

Sexuality: it isn't natural

When I'm teaching about human evolution, some student will almost always ask me what I think is 'natural.' It's a trick question, even if they don't mean it that way.

By 'natural,' I think that they mean 'right' or 'normal.' Sometimes they're worried about something that they're feeling, or just genuinely curious. They may have heard on the news about how homosexuality or monogamy is supposedly 'unnatural' because of evolution. Or they've read where an evolutionary psychologist said that rape is 'natural' or that, actually, humans are 'naturally' mother-centred and poly-amorous, having many sex partners, because bonobos or gorillas or chimpanzees are that way.

The problem is, if the antonym of 'natural' is 'human-made,' how can anything associated with humans be 'natural'? I'm not just talking about sexuality, but about emotions, 'maternal instinct,' supposedly 'innate' preferences for certain foods, aggression, inequality...

I try to tell my students that I don't think we've been 'natural' since we became human. If we are *the self-made species*, why would our sexuality — or our diet, or our social life, or anything else — be any different?

And if life is by nature diverse, if diversity and variation are, in fact, the *precondition* for evolution, inherent in how every living thing is born, then why would any one way of being male or female, married or sexual or anything else exist? Isn't our variation the only insurance we have against changes in selective pressures?

And why should peeling away what makes humans human, complicated, get to what is 'naturally' human? Would peeling away language get to humans' 'natural' ways of thinking? No, it would actually deprive us of one of the things that most makes us distinctly human.

Students are never happy with my answers to this question. They're convinced that there's a thing called 'human nature'. So let me try a different tack to answer the question.

Robert Sapolsky is a brilliant neuroscientist with a background in biological anthropology. Bob studies, among other things, the way that brains and hormone systems work in baboons. If you're interested, you should definitely check him out on YouTube because he's a fantastic lecturer.

Sapolsky tells this amazing story about how he had been studying a troop of baboons for years. They were sort of normal for baboons, with the dominant males behaving horribly, battling each other for supremacy, beating up subordinates, attacking females, feuding with other troops, and generally making life hell for the other baboons. Then, the dominant male baboons took over a trash dump near a resort; they wouldn't let any of the lower-ranking baboons near their tasty trash. But they caught bovine tuberculosis, so that the most aggressive males were wiped out in a single epidemic.

Sapolsky was devastated; he thought his fieldsite might be ruined. He had been tracking the hormone levels for markers of stress for years. The troop now had its gender ratio totally screwed up, with twice as many females as males, and only the submissive males from before the epidemic survived.

But here's where it gets interesting. The male behavior in the troop changed, and that change persisted even when all the males in the group had been replaced more than seven years later. Baboon males switch troops, so the troop is always recruiting. New male recruits to the group didn't follow the nasty dominating male type, but all acted like submissive males. New interaction patterns had been set up. Males were less aggressive; they groomed the females — kind of like the baboon equivalent of gossiping and backrubs rolled into one.

And the baboons stress levels, measured by their hormones like cortisol, were lower. A change in the group's interaction pattern, which remained stable even as the members changed, caused a biological change in its members, including how they acted male and female, how they raised children, how they mated. The aggressive pattern of male dominance typical of baboons was missing.

The point is that, even with an animal much less complicated than us, expectations and interactions have profound effects, not just on behavior, but even on biology. Our relations are not just determined by the need to reproduce or hardwired into our instincts; rather, we reproduce in a social environment, which shapes how we do it. Living things adapt in their behavior, especially brainy living things, they don't just act out fixed scripts.

Anthropologists like to draw a distinction between biological sex and cultural gender: sex is the equipment you're born with; gender is the set of norms and expectations that you think go with that equipment, but is really taught to you by your culture. The distinction is messy, and some traits seem to blur the boundary, but it's useful.

Being male or female in different places doesn't necessarily entail the same ideas about what is masculine or feminine, and these ideas have consequences. Or as anthropologist Agustín Fuentes puts it, with humans, who we think we are matters. It shapes us, our behavior, our children, how we interact...

'It turns out that in many primates sex is not only complicated, it is also frequently not associated with reproduction. Many primate species (especially our closer relatives, the apes) use sexual activity as part of their social repertoire. Social sex can make friends, break friends, end fights, start fights, all in addition to the fact that sometimes it also ends up in reproduction. Social sex is an important part of being a primate. It is no wonder that primates have more sexually transmitted infections than most other mammals…they have more sex.' (Agustín Fuentes, 'Why Is Sex So Complicated?')

Even in our societies, gender expectations have changed over recent generations. And many of the traits that we think of as inherent — the core of being either male or female — often turn out to be more flexible on closer inspection, even though they seem natural to us.

Gender roles don't *feel* variable to us; they feel essential, unchangeable. The irony is that our very adaptability makes a social pattern that is malleable feel like it's inevitable and unchangeable precisely *because* we've adapted so well to it. But that tells us more about how we think and adapt, less about how we innately are or must be.

Sexuality 2: getting busy

You can't control what you're attracted to, no matter how you try to talk yourself out of it. Man, would life be easier if you could!

It's one of the great tragedies, but also the really amazing things about humans — we seem drawn together, not just to reproduce, but even to try to build lives together, no matter how much pain or discomfort it can cause.

Some evolutionary theorists argue that we are 'programmed' with particular sexual preferences or mating patterns by evolution in order to assure reproduction. They think that men and women come into the world with a strong set of preferences for the best possible partner who will help them pass on their genes.

I think that the preliminary data on this isn't that strong. We know that, around the world, and even within our society, everyone's preferences are not the same; some people are attracted to members of the same sex, or even to *no one at all*.

Thank God! I say. If we all had the same preference, we'd all be chasing after the same person, and it would be even worse than it already is.

In fact, if we look closely at the evidence about human fertility, the most important thing to point out is that sex and desire are simply not the limiting factors. The human desire for sex is, to put it bluntly, excessive — from an evolutionary perspective — we've got *more* than enough desire to get reproduction done.

Humans are interested in sex when they're not fertile and have no chance of producing viable offspring. Other animals generally mate when their bodies tell them that they can conceive; humans do it all the time. And we're interested in sex acts that have absolutely zero chance of producing an offspring. Whenever someone says that sex should only be for reproduction, I find it hard to take seriously. They do realize what they're going to have to give up? How little sex we need to get that job done?

Let's try to put some numbers to it: among our ancestors, women were likely to be functionally non-fertile for about four years after giving birth, maybe even more. Our female ancestors probably, like most hunters and gatherers, nursed frequently, day and night, which suppressed fertility. Throw in nine months of pregnancy, an active lifestyle and low body-fat percentage, and they probably were able to have a child every five years.

We call that birth spacing, and it's not out of line with other great apes: orangutans, for example, have even longer birth spacing and even lower fertility.

Researchers estimate that having heterosexual, genital-genital intercourse randomly during a woman's cycle is a little more than 3.5% likely to result in a pregnancy. So, if you assume a possibility of miscarriage, figure our female great-great grand ancestors would have had about a 30-year reproductive life or so at most, you're looking at 5 to 7 pregnancies.

High end of the estimate: 7 pregnancies, 3% chance of getting pregnant... you need 250 or so heterosexual, reproduction-style sex acts —over *your entire lifetime* — to get close to your maximum baby-making potential, if you're a woman living in those conditions. You do the math, but it's not a lot of sex. Less than 10 times a year, on average, with a lot of variation and some really, really long dry patches.

I don't think humans have *ever* had that little sex. In fact, large-scale surveys in the US suggest that even long-term married couples who are not trying to conceive have more sex than this. The point is simply that human desire is not in short supply; it's the babies that are limiting our reproduction.

In other words, and to make this a lot simpler, some of us are having a lot of extra sex, a lot of sex that we know damn well won't lead to reproduction, doing acts that can't lead to reproduction, in combinations that will never produce children. And our ancestors probably did *exactly the same thing*.

Consider one of our closest cousins, the bonobo or 'pygmy chimpanzee,' an animal beloved by anthropologists. Bonobos engage in all kinds of non-reproductive sexual activity, in every conceivable combination — female-male, female-female, male-male, female-child, female-female-male-child... you get the idea. Whereas the common species of chimpanzees builds social relations through grooming and aggression, bonobos seem to use sexual interaction to settle fights, introduce themselves, calm their nerves, say 'hi' to a friend...

We're not bonobos, but bonobos show us that sex can be exapted or repurposed for all sorts of other jobs: we use it to bond with our partner or close allies, to feel good, express ourselves, ...

I think it makes more sense to realize that sexual behavior in humans, like in other animals, is flexible and adapts to a situation.

We know that the pattern of mating in humans varies. For example, we find that a number of societies practice polyandry — one woman taking multiple husbands — many more than what Western anthropologists once thought. It seems to be a pattern that arises when women are in short supply. And men often change their behavior if they are in male-only situations, like at sea or in prison. Some societies even assume that a person's sexuality will change over time, transitioning from one preference to another, or fear the opposite sex. Fortunately for our continued survival, we have more than enough sex to get the job done, no matter what crazy ideas we get about sex.

The thing is, this is not how we think about our sexuality or how it *feels*. Our preferences feel to us to be innate, ingrained, and utterly unchangeable. Our preferences — for one type of relationship, for one way of being a man or a woman, for a particular sort of physical interaction, for a partner who looks a particular way — may feel like an essential part of us because they are; sex is a crucial way that we define who we are, an activity almost as important for humans as eating and drinking.

But we also confuse ourselves, mistaking the way we think things should be for the way that they actually are. We think in norms, or ideals.

The norm of an institution like marriage is a complicated brew including religion, tradition, economic relations, property and divorce law in a society. It's a bit of a fantasy, but it's a fantasy that we try to impose on a very messy reality.

For example, a classic survey of anthropological research found that 84% of all cultures allow or encourage polygynous marriage: a man taking more than one wife. But even in those societies that *most strongly encourage it*, the majority of men don't have polygynous unions; for most, the cost is simply too high. Besides, you do the math; it's simply impossible unless a society figures out how to change the ratio of boy to girl babies.

In summary, 'sexuality' is not the same as sexual behavior. Once you have complicated ideas about sex, ideas that shape your choices, you've got a really human way of being sexual. And like the social apes that we are, we find it almost impossible not to worry about what sex other people are having, how they're doing it. You can't look to what's natural to clear away the mess, because the mess is what's natural.

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James Trussell of Princeton University has pointed out that the probability of becoming pregnant is a bit more complicated than my back-of-an-envelope estimate. He and his colleagues, Germán Rodríguez and Charlotte Ellertson, in research on emergency contraception, estimate that, if a woman had a 28-day cycle and randomly had intercourse once in that cycle, her probability of pregnancy would be, on average, 3.82%. In order to be 95% certain of achieving conception in a year (assuming this 3.82% rate), a woman would have to have sex approximately 77 times. Of course, in many cases, a woman would get pregnant on fewer attempts, but Trussell and colleagues suggest that my estimate, although close, might be a bit on the low side.
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References & resources

Key concepts

Sexual reproduction provides species with a number of benefits, including variation through genetic recombination.

Sexual selection acts on the sex that is not the limiting factor on reproduction, and can take the form of either direct competition or mate choice.

Human reproduction is shaped especially by the extremely altricial nature of human infants; many social innovations seem to help our ancestors achieve shorter birth spacing and higher-than-expected reproduction rates.

Sexual behaviour seems to be exapted into new forms and new functions, beyond simple reproduction, in most species.

Human sexuality has been variable for a long time.

Resources

'Wild Sex,' series of web videos hosted by Dr. Carin Bondar on sex and reproduction across species. (Beware: some content is not family friendly, but it's all educational.) (link)

Marriage and Other Arrangements. Open Anthropology, 1(1) April 2013. Collection of classic anthropology papers on marriage, monogamy and related issues from the archives of the American Anthropological Association. (link)

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Brains

Among all our traits, the human brain stands out as peculiar. Although our intelligence may appear to us to be an unqualified good — an all-purpose adaptation — the rarity of extravagantly oversized brains makes us wonder how evolutionary pressures could produce such an outlier, especially given its cost to us. Moreover, once our ancestors had out-sized brains, how did this affect evolution?

What are brains for?

What are brains for? Why don't we ask the sea squirt.
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The sea squirt is a simple animal. It starts life as a larva in the sea looking like a tadpole. This phase of its life is brief, however; the larva searches for an ideal place to anchor itself on the ocean floor and then fastens itself where it will spend the rest of its life, never moving again.

The sea squirt eats by filtering water, catching suspended particles. They're hermaphrodites — they've got both male and female reproductive systems. They reproduce by squirting their sperm out and letting the currents carry it to the ... other... lucky... sea squirt.

But what's really interesting about sea squirts is that they are chordates. That means they have a basic nervous system, even a kind of eye in some species. While they scout for a place to cement themselves to the ocean floor, they have a basal ganglion, a cluster of nerves like a simple brain. Once they're planted, however, they start their adult lives, and *digest* their own brains and nervous systems. They no longer need a brain, so it's the first thing that they eat as adults.

The point is simple. No, it's not that adults have digested their own brains...

We may be impressed by our cognitive abilities, by our logic, creativity and advanced intellectual skills. We may think that brains are for creating language and symbols, for imagining, building technology, or plotting deviously against each other. But that's not why we have brains, from an evolutionary perspective. We know this because lots of living things have brains that can't do these sorts of complicated cognitive tasks.

From an evolutionary perspective, we have a brain for two reasons, both linked to survival. First, if you don't move, you don't need a brain. The sea squirt shows us that. Brains are for interacting with the world. If you don't perceive the world, or need to react to it in order to eat or mate or defend yourself — no brain. Trees and plants don't need brains because, even if they could perceive their surroundings, they couldn't do much about it. And they get along perfectly well.

Second, brains regulate bodies. They help an organism to achieve homeostasis, or healthy balance. Lots of living things do this without a brain, but a brain can really help, especially if your needs are complicated and your system needs some executive control. A brain is your body's way of telling yourself, 'I'm hungry; I'm going to go eat,' or 'It's too hot here; let's go in the shade,' and then *doing* something about it.

We are separated from other animals by what may appear to be a mental chasm, a *huge* gap. We have a host of cognitive abilities — language, abstract thought, powerful abilities to learn, self awareness — that other species seem to only possess minimally, if at all. We may be more than 98% similar genetically to chimpanzees, but whatever is in that 2% must be pretty important.

When we look more closely at our brains, what we find can be startling. Like our forelimbs, our brains are also full of homologies — in fact, we cannot find a part of the human brain that is not present in other species. The size and shape and functioning have changed, sure, as we'll talk about in the next lecture, but there's an enormous amount of consistency across species.

Once upon a time, for example, brain researchers went looking for the part of the brain that allowed us to speak. They assumed that, because only humans could do it, we must have some special language part of the brain. But the two regions that are most associated with language, Broca's and Wernicke's areas, both have homologues in chimpanzee brains. They just get used for other purposes.

The structure of nerve cells is so consistent across living things that we can take brain tissue from one species and implant it in a totally different species. If we do it early enough in development, the implants will get incorporated into the animal's brain, what we call a chimera.

As with so many other parts of our body, evolution has not invented something wholly new but rather tinkered with existing structures to produce innovative capacities. If there is a gulf separating our cognitive abilities, there is also a shared foundation of brain building blocks.

For this reason, we can really learn a lot from studying the brains of other animals because of what we share with them. We can also see the ways we differ, how parts get and adapted, to help us to understand what allowed our ancestors to survive and become the way we are today.

So, to start off with, we need to remember the lesson of the sea squirt: when we look across all species, brains are for moving and interacting with the world, not for silently reflecting or deep thinking. Because of this, humans are good at some tasks, lousy at others, even though we might not realize it.

The philosopher Andy Clark has said that our brains are, 'good at Frisbee, bad at logic.' It's a great point. You may not realize it, especially because we're told our brains are like computers — memory or logic machines — but you're actually not really all that good at remembering or at logic. One of the reasons that computers or smart phones are so useful is that our brains don't work like they do — your phone is probably much better at remembering phone numbers than you are! Your computer is much better at logic and calculation than you are.

In contrast, you're likely really good at perceptual and motor tasks, pattern matching and face recognition, for example, and possibly even frisbee. These tasks turn out to be really, really hard. It's very hard to get a computer to do them. We've learned this, in part, from robotics. It was relatively easy to build a computer that can beat a human at doing math operations, but have you seen the robots that they have tried to build to play soccer? They couldn't play for the local under-10s soccer team!

Brain functions, old & new

We have to realize that brains were built by evolution, not to think, but to survive in the world. We tend to be good at tasks that mimic the sorts of challenges our ancestors faced, or that we can transform into these kinds of jobs, finding a way to hack around our cognitive limits.

My friend at Macquarie University, biologist Ken Cheng, teaches about simple animal brains to make this point. Among other things, Ken studies ants. He likes to point out that animals can sometimes do amazing things with very small brains. Some can even do things that we can't do with much bigger brains, because of the way that evolution has shaped their mental equipment.

Ken discusses *Cataglyphus fortis*. *Cataglyphus* is a type of ant that survives in the desert, in temperatures up to 50 degrees (that's 122 Fahrenheit). They eat other insects that keel over in the heat.

What's amazing about *Cataglyphus* is that, when it goes wandering around on the hot sand or in a saltpan, it must look to the ant like a totally featureless landscape; the ant might as well be walking on the surface of the moon. The ant will wander this way and that, weaving around, searching, with no landmarks on the ground to guide them back to the nest. When it comes upon some food, like a fly that's died from sunstroke, it grabs the food and rushes straight back to its nest. Even if it's a football-field length away from home, and been wandering for a while, *Cataglyphus* will barely take a stray step.

What *Cataglyphus* has done is an example of highly modular intelligence. Its brain is incredibly good at remembering how to get home, remembering each step, adjusting for the direction, and then adding up all the little steps to figure out the path straight back to the nest. Its eyes perceive patterns of light in the sky that are invisible to us so that it always knows which direction — north, south, east and west — it's stepping. The evolutionary pressures of living in the desert have shaped a brain that is really specialized, but *Cataglyphus* isn't good at learning new tricks.

Some brain researchers argue that the human brain, too, is built up of 'modules,' special-purpose cognitive tools that do a very specific task. In fact some of human intelligence may work this way; for example, we may have special purpose modules for essential tasks, especially social jobs, like understanding what other people are doing, imitating them, or detecting each other's emotions.

One of the interesting things about humans, however, is that, even with our most specialized cognitive tools, we can often do quite strange things and build up new skills from old modules. We repurpose or exapt some of the most basic brain tools into new uses; some cognitive theorists call this neural reuse or neural recycling.

For example, when we learn to read, we train parts of our brain that could not *possibly* have evolved *for* that task. Reading is just too new for a specialized part of the brain to have evolved. We know, instead, that parts of the brain used by animals to recognize basic shapes get repurposed in people who learn to read to pick out letters quickly. This kind of neural reuse is widespread in our brains, and it involves both some of the newest zones of the brain and some of the most ancient.

One thing we have to realize is that evolution has achieved some cognitive advances by adding functions onto some brain areas, and layering new levels of control on old systems.

For example, some of the oldest, most important areas of the brain, shared by virtually all animals with a nervous system, are right at the top of the spine, at the brain stem. The brain stem controls essential functions — breathing, swallowing, sleeping, pain perception — and it connects your brain to the peripheral system so that you can feel and control your muscles. It's ancient, but it's also absolutely critical. Damage a part of the neocortex of your brain, the outer layer, and you'll get some weird memory or function losses; damage the brain stem and you'll be lucky to be conscious or breathing.

These parts of the brain are highly conserved across different species; evolution doesn't mess too much with the control system for breathing or making the heart tick.

However, in humans, we actually find that we can override some of these automatic systems, or drive them with new inputs. For example, we can drive ourselves to panic so badly that we have trouble breathing and our heart races as if we were under severe threat, even when we're just watching a horror movie, or remembering a stressful event, or seeing something that tips off a phobia. There's even amazing examples, like being able to hold our breath and talk, where we override one of our most basic automatic functions — breathing — because of the power of other parts of the brain. We'll discuss this stuff in the next lecture.

It's been really important in our evolutionary history that the perfectly sensible automatic responses of the midbrain and brainstem can get over-ruled, and that these responses, such as strong emotions, can get recruited for new uses. Our early ancestors who made the move from vegetarians and scavengers to hunters eventually had to overrule the most reasonable demand of the automatic system to run like mad when a large animal started to run toward them. It took an enormous act of imagination and self control to see a charging animal as a potential meal and keep steady.

We recruited our basic responses into a whole new cognitive world: we learned to fear or love imaginary creatures, suffer pain from disappointment, and long for justice or other abstractions, not just a meal, a mate, or a place to sleep. We haven't evolved beyond 'primitive' impulses; if anything, we've given them countless new targets, everything from lusting after new technology to feeling real emotions when daydreaming.

One of the most widespread myths about the brain is that we only use a small fraction of it. Nothing could be further from the truth.

We are constantly using virtually all of our brain, even if we're not consciously aware of it. The vast majority of our brain functions are going on without us knowing, but they're keeping us alive. Your brain is running your body, adjusting your organs and hormone levels, tinkering with your muscles and posture constantly, and, occasionally, pointing stuff out to your attention, alerting your consciousness to check something out.

Your brain is doing what your ancestors' brains always did; keeping you alive in more ways than you even realize.

Bigger isn't always better

Size matters. When it comes to brains, there's no doubt about it.

And humans have very large brains. Although there's some variation, we average around 1200 or 1300 cubic centimeters or 'cc's; that's about 1.5 kilos, or three pounds. Compared to our earliest known hominin ancestors and to the other great apes, our brains are triple in size.

However, if brain size alone determined intelligence, we'd expect elephants, dolphins, and whales to be far smarter than we are. Elephant brains are about three times heavier than ours; a sperm whale's, about six times.

Researchers who study brains across different species talk about encephalisation. Encephalisation is the mass of the brain compared to the body. The clearest pattern emerges if you log the two weights, that is, don't treat them as a straight 1:1 relationship. As an animal gets bigger, its brain gets bigger too, but more slowly. It makes sense if you recognise that a lot of the brain is responsible for keeping the body running and controlling organs. Just because an animal gets larger doesn't mean it gets another heart or a couple more pair of lungs for the brain to look after.

Some of the smallest animals have brains that are very large as a percentage of their body; for example, the brain of the pocket mouse is 10% of its total bodyweight. In contrast, the sperm whale has a giant brain, tipping the scales at almost 8 kilos (about 17 lbs.), but since the whale can weigh over 40,000 kilos, or 45 tons, that 8 kilos is a bit less impressive; it's about .02% of its bodyweight.

If you plot these comparisons, you find that they tend to be consistent for different branches of the evolutionary tree. Most vertebrates, like lizards and fish, are at one level of encephalisation; mammals are on a slightly higher curve. With a mammal and a lizard or a fish of the same weight, the mammal will have a heavier brain. Mammals seem to be more 'encephalised,' or brainier, kilo for kilo.

We know that predators tend to be brainier than their prey; prey that actively evades predators brainier than prey that just hangs out and hides. And diet and parenting style also correlate with difference in encephalisation: fruit eaters and careful-parenting species often have larger-than-predicted brains. Some of the most overly-well-endowed animals are those with complex social lives.

Primates have an even higher encephelisation ratio than other mammals. But humans stand out as an outlier, even among the primates. How much of an outlier depends upon which species you compare us to. Even next to other really brainy great apes, we've got two or three times more brain than you'd expect given our weight.

Go back three million years ago, to the remains of *Australopithecus afarensis*, one of our hominin ancestor, and you find a skull that still looks about the right size for a great ape: smart, certainly, but not much more than a chimpanzee, probably. We're pretty confident Australopithecenes were clever enough to use tools, but so are chimps, and even gorillas.

If you look at 'Lucy,' the most complete *Australopithicus* skeleton we have, the most dramatic differences between her and a chimpanzee are from the neck down, not up in her skull. She was probably walking like a modern human, but she was still like our ape cousins above her neck. Our hominin ancestors learned to walk upright before they really became strange neurologically.

If we follow our ancestors from Lucy forward in time, towards modern humans, we see a really startling changes. The brain size of our ancestors didn't grow steadily; it spiked, apparently as a result of pretty intense selective pressure, or a relaxation of a constraint, or some combination. Brains got big fast, at least from an evolutionary perspective.

The real increase in size, the break that created a brain different to other apes, starts a bit before 2 million years ago. The remains we find from this time, usually referred to as *Homo habilis*, have brain cases that are about 30-40% larger than earlier hominds, up to about 600 ccs, at first. But over the next 300,000 or so years, things start to change quickly.

By about 1.7 million years ago, we find evidence of a species we call either *Homo erectus* or *Homo ergaster*, with brains as large as 900 cubic centimeters. There's a lot of variation around the average, a lot more than you find today, but the trend upward is clear and quick. You're probably thinking that 2 million years isn't so fast, but this is a huge change for this kind of time frame.

Before I go on, anthropologists argue about naming and whether or not some of these are separate species, and what to call them, but I won't get into that. I don't want us to get bogged down in a lot of names, dates, and debates. If you're interested in this, and want more, I'll post some great links for you to explore. The important thing for our discussion of the brain is the trend over time and to understand why it might have happened and how.

Some of this growth in brain size appears to be a result of an overall increase in body size; *Homo habilis* was a bit bigger than Australopithecenes, and *Homo erectus* was even bigger: about as tall as a modern person. But not all of the increase in brain size can be explained as just the scaling of the brain along with the body.

Back 1.5 million years ago, *Homo erectus* still had some ape-like traits in its skull, although its lower body looked modern, only tougher and more robust. They had smaller teeth — closer to ours — flatter faces, less sexual dimorphism, longer legs and bodies better built for walking, even running. But they also still had heavy ridges over their eyes, no chin or forehead, and their brains were still shaped more like an ape's than ours.

Homo erectus was incredibly successful. The species lasted about a million and a half years, spreading out of Africa into Asia, and maybe even into Europe. They may have been the first hunter-gatherers in our lineage; in fact, following game may have been how our ancestors first go out of Africa.

To spread like this, they had to adapt to unfamiliar environments, to new food sources, predators they had never seen before, a whole raft of new challenges. They had become an invasive ape, not one tied to a particular ecological niche, and their brains obviously had a lot to do with it. In some pockets in Asia, *Homo erectus* lasted until at least 300,000 years ago, with their brains getting even a bit larger towards the end.

The benefits of immaturity

In our ancestors' tools, we can really see how the changing brain mattered. Up until about 1.8 million years ago, all the tools are pretty simple. We call them Olduwan or 'pebble' tools. They basically look like a river cobble with one side fashioned into a sharp edge by some rough hammering. They're still better than anything any other living animal could do, but if you're not an expert, you might walk by them without even realizing they were tools.

About 1.8 million years ago, someone — either *Homo habilis* or *Homo erectus* probably — started to fashion what we call Acheulean tools. We call them 'hand axes' although they were likely used for butchering and a whole host of other tasks, not so much cutting down trees.

There's two really interesting things about Acheulean tools: their regularity, and the fact that they didn't change a lot over a very long time. It's hard to know for sure about the cognitive abilities of the humans that made these tools — it's hard enough even to a living thing's cognitive ability when they're alive — but they do offer us some clues.

Their regularity is remarkable because it shows that whoever made them was imposing a mental model, an image of what a tool should look like, on the raw material, generation after generation, for about a million years. Whoever made them didn't just whack together something that would work, or do the minimum necessary. One of our ancestors went out and found a proper stone for the job and imposed a design, one that was more symmetrical and standardized than it needed to be, one that had been passed down to them.

I think this shows the way increasing cognitive powers were giving our ancestors a more sophisticated way of conceptualizing tools, learning and teaching, and preserving knowledge.

But, and this is key, too, Acheulean tools show us the limits of this stage in cognitive development. Although you can say lots of nice things about *Homo erectus*, they were not innovative. They got something that worked and stuck with it. You could say that they were good at passing on information and sticking to a model, but got mostly failing marks at improving designs or coming up with new innovations.

Creativity and invention may have taken a bigger brain. But remember: bigger alone isn't necessarily better in hominids either. We're pretty sure that Neandertals, who lived from about a half-million years ago until about 30,000 years ago, and our own ancestors had larger brains than we have, as much as 20% larger. The average brain size of a human has actually been decreasing over the last 80,000 years or so, even more rapidly in the past 20,000 years.

Organization of the brain matters, just as size does. When brains get larger over evolutionary time, every part does not get larger at the same rate; it's kind of like the relationship between brain and body weights. Some parts grow disproportionately.

In the case of primates and humans, especially, the brain structures that have grown disproportionately are the outer layers, or the cortex and neocortex. The parts that control the automatic functions didn't increase as much. I talked about this in the last lecture, how we gain the ability to override perfectly sensible instincts, not because we get a whole new brain area, but because the balance of power shifts when some parts grow disproportionately strong.

Over-riding instincts may not sound like a big deal, but not always acting on your first impulse creates a lot of space for flexibility in behavior. If every time you got frightened, you could only get enraged or panic — fight or flight — you'd never learn to ride a bike, or talk in front of a crowd, and you'd be pretty awful to live with.

These outer areas in the neocortex also do a lot of work making long-range connections in the brain, helping us to build new cognitive associations. The point is not that the neocortex makes us human; all mammals have one. Instead, the disproportionate growth of the neocortex has made it possible to recruit other parts of the brain more easily, do new things with our modules, control these responses better, and even use them to do new tasks.

For example, we have parts of the brain that interpret what we see. They turn a whole diffuse set of visual impressions into a kind of coherent image, and then recognize what an object is. In humans, these visual parts of the brain can be driven, not just by the eyes and sensory experience, but by will and imagination. You can run them backwards, if you will, or top-down. You can think about what an imaginary creature might look like. You can run different scenarios imaginatively in your brain, without having to act them out, prior to deciding what you will do. The increased cortex makes our brains become less automatic, more autonomous and capable of doing what we want them to, even if that's really foolish and counter-productive.

How did our brains get this way? The key is by changing the developmental programs and the way that the brain runs. That is, as we've been discussing, you don't need wholly new genes or brain parts; you need to change the pattern of growth, the connections that emerge, and how the brain runs. That's affected by gene regulation as the individual develops, first as an embryo, and later as a child and adult. And the developmental trajectory of human brains is really unusual.

In most mammals, brain growth is over fairly early. In humans, the period of early, faster brain growth appears to be prolonged. We stay immature longer, which gives our brain, especially the parts that are last to develop, like the neocortex, more time to grow.

In fact, if you look at them closely, human skulls more closely resemble immature chimpanzees' than adult chimps'. If you were a chimp looking at one of us, chimp-you might say, 'What's wrong with these humans? No fangs, no snout, flat face, big eyes, sparse coat... They look like babies! When are those humans going to grow up?' Humans even mature more slowly sexually, and our teeth erupt later.

We call this pattern neotony, the retention of juvenile traits for an extended period of time, even into adulthood. We can see something similar in domesticated dogs, who in many ways are neotonous wolves who hang onto their juvenile traits.

Neotony hasn't just affected our faces; it's also really affected our brains. When humans are born, their brains are only about 25% of their adult weight. Chimps are born with brains about 40% of their adult size. And macaques, who are still pretty brainy compared to other mammals, they've got 65% of their adult cranial capacity at birth. When we're born, chimpanzees and humans have very similar encephalization rates. Humans' brains, however, continue growing at accelerated pace, where chimpanzees' brains slow down.

This long, slow maturation process means that our brains do much of their developing outside the womb, bathed in the stimulation of adult interaction, full sensory experience, and opportunities to learn. We retain youthful brain plasticity, the ability to adapt to new challenges and learn skills more rapidly, for longer than other primates, and for a lot longer than other mammals.

So the next time someone calls you 'immature,' you can just smile and say. 'Yep, that's the way evolution made me.' It's one of the things that makes us human.

Expensive tissue

So, if having a big brain is such a good thing, if staying immature longer is so great for learning, why aren't all animals like us? Why doesn't every animal have a big brain and take a slow train to adulthood?

We, humans, tend to be very impressed by our brains, thinking that they're great for every occasion. Whenever I ask students about what sort of change in an organism would be a good adaptation for some selective pressure, virtually every time, a student will say, 'Oh, a bigger brain will solve that problem.' It doesn't matter what the problem is.

If large brains were so useful, such a 'no-brainer' for evolution, we'd expect heaps more animals to have them. But they don't. Brains the size of ours are rare, even a freakish adaptation, a strange outlier, and one that certainly does not work out for every animal.

In fact, the general rule of brain growth in evolution appears to be that an animal gets just as much as it needs and no more.

The first reason is that brains are 'expensive tissue.' You pay a high price for a big brain, a price in calories. Your brain makes up only about 2% of your bodyweight, but when you're sitting still, it's sucking up at least 20% of your body's energy. It takes a lot of juice to power neurons.

As infants, it's even worse. Towards the end of pregnancy, an embryo's brain is eating up 60% of the calories going into the infant, not just to power the neurons, but also building more and more of them. A shortage of calories during this rapid development can lead to permanent neurological problems.

So we might say that the metabolic price of brains is high; it acts as a constraint on growth in evolution. If a species can't afford a big brain, it won't get it, no matter how nice it might be to have.

For example, gorillas appear to have gotten larger since we shared an ancestor with them without their brains keeping pace. Their bodies have grown, possibly due to sexual competition, and their brains have lagged behind. The problem is, a gorilla already has to eat about 80% of the daylight hours to get enough calories to survive, and they don't even move a lot — maybe only a kilometer or less each day.

A gorilla would have to get another 700 calories or more a day to get enough energy to support a human-sized brain. There simply aren't enough hours in the day to chew up that many leaves.

One additional problem for our ancestors in the past few million years, though, is that usually when an animal needs more calories, it also develops a better set of equipment to get that energy. If a species grows a larger body through selection to defend itself or to fight for mates, it usually gets a larger jaw or bigger gut to pull in enough calories to feed that bigger body.

Our ancestors, however, went through the opposite process: in *Homo erectus* and even more so in *Homo sapiens*, our ancestors' teeth got smaller and smaller, their jaws shrank. We can see this clearly in their skulls: the way that the cheekbones grew smaller and the sagittal crest, the ridge on the top of the skull, gradually disappeared as the jaw muscles shrank. As the brain case was getting higher, rounder, larger — marks of a bigger brain — the indicators of big jaws and powerful teeth were disappearing — some theorists even say that the brain case could only grow because the jaw shrank.

The growing brain, the shrinking jaw and a small gut made the food problem big, really big. Primatologist Richard Wrangham has argued that you simply can't grow a human-sized brain on the diet of a gorilla or chimpanzee; our ancestors had to change what they ate. Gorillas, for example, are mostly raw food vegans; they eat leaves, fruit, and no doubt the occasional insect. Chimpanzees prefer fruit, but aren't as picky, but they still only get occasional snacks of meat, perhaps less than 5%, maybe as little as 2%, of their calories.

Wrangham, who's studied the evolution of diet, argues that, if our ancestors had stuck with a chimpanzee-style diet, they would have had to eat 5 kilos of raw plant food each day; that's about 11 pounds of fruit and veg. They'd have to chew 6 hours a day, minimum, even before they got to modern brain sizes.

In contrast to the other apes, humans are truly omnivorous. We eat a really wide variety of food. Animal protein — meat — makes up anywhere from a quarter to nearly 99% of the calorie intake of the foraging peoples studied by anthropologists around the world.

Why does this matter? Meat has more energy per kilo. To get the same calories you would get from eating a kilo of lean game meat like kangaroo, you would have to eat about twice as much fruit like grapes. And you'd have to eat about 7 kilos of a leafy green like kale to get the same energy.

We suspect that two million years ago, *Homo erectus*, already bigger brained but not yet human, began to have an increasingly modern, varied diet. Big brains required rich food if you didn't want to sit there eating all day. *Homo erectus* likely started to eat a lot more meat, maybe just scavenged at first, but later hunted. Nothing about our bodies looks like a straight-up carnivore; our guts are way too long and our stomach not nearly acidic enough. Our ancestors had gone from being herbivores gradually to becoming high-yield omnivores; they were foraging widely, and may have even cooked their food.

Cooking makes food easier to eat and digest. Cooking concentrates the calories and cuts down the effort to chew, outsourcing the food processing duties from our jaws to our technology, hands, or fire.

But it wasn't just meat or cooking alone that made the difference; our ancestors also got better and better at spotting high-energy foods of all sorts, and then pre-processing them before eating. They were substituting wide-ranging, high quality foraging — walking around finding the most high-calorie meals — for short-range, low-quality grazing — like the gorilla, just sitting their eating what's around you. This involved learning how to get energy-dense treats like honey, shellfish, more nuts, eggs and even stealing caches of food left by other animals.

Our ancestors eventually, later, learned when seasonal sources of food were available, like stands of fruit, migrating salmon, or calving animals. They had to devise new ways to exploit these, especially as they spread into unfamiliar regions, and teach their young to do the same. That is, their brains were hungry, demanding, but their increased intelligence opened up ways to get foods densely-packed with the calories they craved.

By the time the first modern *Homo sapiens* show up a bit less than 200,000 years ago, we see the beginning of a 'broad spectrum' approach to diet. No longer strict vegetarians, no longer big game hunting specialists, they were building versatile tools that suggest they were learning to fish and trap, developing projectiles like spear-throwers and eventually bows and arrows, sewing, trading over longer and longer distances...

I always warn my students who are interested in a 'Paleolithic diet' that our ancestors' menus probably would have turned us off — that is, unless you really like insects, worms, small raw vertebrates like lizards, and basically eating anything and everything edible that you can lay your hands on. Our ancestors probably were not terribly picky. We know that most foragers studied by anthropologists actually eat a more varied diet than most of us do, eating scores of animal protein types, a lot of them small animals, for example. Bon appétit!

Even brains have limits

Bipedalism helped make this diverse, high-yield diet possible. Walking on two legs is more efficient over long distances than getting about on all four: 35% more efficient according to some research. We spend less energy moving around, going further on the same tank of fuel. If you're living where food is scarce and widely spread, that extra range might be the difference between getting something to eat and going hungry.

In addition, walking on two legs freed up our ancestors' arms to carry food. They could have ranged far and carried what they found back to a home base to share. Chimpanzees and gorillas don't have to travel far each day to find enough to eat, and they're not good at sharing; our ancestors likely worked together better.

It wasn't all easy going, however. Scarcity would have stalked our ancestors constantly. Especially in the period from around 800,000 to 200,000 years ago, a time when some paleoanthropologists think that the human brain might have gotten larger more quickly, they would have faced some serious climate fluctuations. They would have to endure waves of cold and dry ice ages and wetter, warmer periods.

For the most adventurous bands of hominins, those families who moved to the fringe of their habitable range, shifts in the climate ramped up the selective pressures. When we look at our bodies, we see not just the effects of plenty, but also hunger shaping our ancestors, such as our uncanny and frustrating ability to lay in a store of fat whenever we get a chance. Dietary versatility also may have been one way that they survived repeated waves of starvation.

Brains pose other challenges, however, not just diet. A large brain cranks out heat. Any time living tissue consumes calories, it also warms up, so we know from the brain's appetite for energy that it's also going to have had a cooling problem. In fact, one of the greatest dangers of heat exhaustion and sunstroke is that your brain can roast, potentially killing you. Your brain is the weak link in your body's thermal system.

Our ancestors' bodies adapted to deal with heat in a number of ways: they lost a lot of their body hair, multiplied the number of sweat glands, and even rerouted blood into the skull. The blood bathes our brains and draws off heat, pumping it throughout the rest of the body, like a kind of radiator system.

Being bipedal also helped our ancestors to keep cooler. Standing up puts more skin into contact with a breeze, and cuts down on how much sunlight hits a body when the sun is high. You may have experienced this if you've ever been lying on the beach, getting really, really hot, but stood up, and found that you were suddenly much more comfortable. And there was a breeze you didn't even know about! The air moves more a meter or two off the ground, and you're much less of a solar collector when you're standing up — the same factors may have helped our ancestors to overcome the constraint posed by brain heating.

One of the more controversial theories, but one that I quite like, is that this advanced cooling system didn't just keep us alive, it helped us to go from long-distance walking to running. According to anthropologist Daniel Lieberman, we didn't just evolve to walk; our bodies are well built from running long distances without having to stop. Other animals run much faster, but they have to stop periodically or they risk over-heating.

In contrast, humans can run and run and run without stopping, even in the heat. Our ancestors might have developed the capacity to be 'persistence hunters', literally running prey to death. Some hunting people can still do it. The trick isn't to go fast, it's just to prevent your prey from resting and cooling down. Eventually, if the animal can't stop long enough to bring its temperature back down, it will simply pass out from heat stroke.

Our brains, however, aren't just a challenge because of the heat and the need for energy. The slow development of our brains, although it makes more learning possible, also imposes its own costs. A human baby is a bit like an extra-uterine fetus; even basic motor control and the senses are undeveloped. Because our brains have only achieved about a quarter of their final size when we're born, our nervous systems are especially underprepared for life outside the womb. And that slow maturation process, although it creates opportunities to learn, places an extra, long-term burden on the adults who must care for the baby.

The pattern of growth means postponing sexual maturation, increasing the risk that the child dies before passing on its genes. If our ancestors' mortality was higher, the risk would have been too great, and the slow growth trajectory would not have been possible. Some researchers even think that this slow development makes humans more susceptible to brain disorders, especially those that don't seem to show up in other animals.

Finally, big brains also have certain inherent engineering problems that come from the way that they've evolved. The signaling mechanism we use — all animals with brains use — is about 600 million years old, and may have evolved first in a kind of jellyfish that didn't even have a brain. The bigger the brain gets, the harder and slower it is to move messages around. The more neurons you get — what we call gray matter — the more you need connecting material, or 'white matter'. The connections actually increase more quickly than the number of neurons because there's a lot more connections needed for each extra bit of neurons.

In humans, the number of connections hasn't kept pace with the number of neurons, so our brains are less densely-connected, in some ways, than simpler brains. This creates some quirks for the human brain; lower communication density means that local areas of the cortex can specialize more, which may create more cortical zones, so that we can learn more skills, more complicated behaviours. We've also adapted by splitting up our brain functions even more between the two sides of the brain, the right and the left.

The bottom line is that, like every other part of the body, the brain has limits and imposes costs. We may tend to look at 'em and think, 'Man, our brains are great,' but they've also been a real burden. Without our technology, our intelligence, our sophisticated ways of getting food, and our ability to cooperate, we wouldn't be able to afford to pay the evolutionary bill on these brains. The price would simply be too high. That's the lesson other animals, with their smaller, less costly brains teach us. Whatever's most unusual about us, in some sense, needs the most explanation.

Brains change everything

Brains change everything. They affected the selective pressures our ancestors faced, our patterns of inheritance, even our likelihood of surviving into the future.

But one of the most curious things about our big brains is that, although our ancestors looked very modern in the brain case as much as 170,000 years ago, it really still took them a while to start acting fully modern. Finally, about 50 to maybe as long ago as 70,000 years, they came out of Africa, and by 30,000 years ago, they were already surviving on the cold coasts of the Arctic Ocean. How did they get so smart, but also, why did it take so long, if the brains were just as big 100,000 years earlier?

To really understand how our brains affect us, we also have to think about why we got them. Their origin helps us to understand how bigger brains eventually, eventually, lead to sophisticated, modern lifestyles.

There are two basic types of theories that explain how we got such large brains: environmental and social. There's variations in each, even combinations, but the question is really what role do we think external factors or selective pressures had, and to what degree internal factors, competition among humans, drove changes in the brain.

Environmental theories often follow along the lines that we've already been discussing about the brain and diet. According to these theories, a change in brain size allowed human ancestors to change their foraging behavior, or shifted the relationship between our ancestors and the environment, like the way that humans dealt with predators or climate change or some other external factor.

The improved diet, for example, had a kind of cyclical effect; it demanded greater intelligence, memory, and problem solving, but it also provided the calories that we needed to feed a bigger brain. Throw in scavenging meat, and eventually hunting, and invading new ecological niches, tool use, cooperation, and a whole range of cognitive skills, and you've got a big payoff, a complete shift in how humans relate to external selective pressures. These are all environmental explanations.

I don't think there's any way to dispute the importance of external relationships in brain evolution — diet, self-defense, expanded range, resilience against climate change. However, the ecological model alone doesn't seem to explain the large brains: if ecological forces, alone, drove brain evolution, you'd expect that other animals that went through the same sorts of processes might also wind up with big brains.

There were lots of other animals around in Africa going through the same changes, even other apes, but they didn't get this spike in brain growth that we've seen in humans in the last 2 million or so years. Also, our ancestors had the big brains before they really had the complex foraging behaviors that eventually allowed them to spread throughout six of the seven continents.

Increasingly, many evolutionary theorists think that we can't really understand that spurt in brain growth or the slower effect on our ancestors' behaviour unless we focus on social forces. Social forces are forms of intraspecific competition, that is, human against human, not just human against environment. Our brains got bigger, not because of the cognitive demands of our diet or disease or climate or predators, according to social explanations, but because we used our brains to compete with each other.

One of the earliest versions of this theory was known as the 'Machiavellian intelligence' hypothesis, after the political philosopher Nicola Machiavelli. Machiavelli wrote a book called The Prince in the sixteenth century that offered cold, ruthless, calculating advice to a political leader, how to use cunning to stay in control and expand his power, with every strategy at his disposal.

Primatologist Frans de Waal, who studied chimpanzees, first pointed out that their social lives demanded strategic skills, alliance building, conflict negotiation, and deception. De Waal wrote that chimpanzees needed Machiavellian cunning, just like humans.

It's not just that primates lived in groups; ants lived in large groups too, and they didn't get particularly intelligent. De Waal and other theorists recognized that primates scheme and cooperate. The idea is that the complex and shifting nature of primate daily life, the fluid structure of rivalries and changing alliances, taxed our ancestors' intelligence. As hominins or other apes grew smarter, they became more devious in 'everyday politics.' We now generally refer to this as 'social intelligence' theory, especially as cooperation is just as important as deception.

Social intelligence theory suggests that human brain evolution has been driven by a cognitive arms race among our ancestors, especially most recently, as the most socially adept out-performed those who couldn't keep up. Brain growth was driven by social cognition.. If you want to look at it this way, our obsessive interest in each other's business, gossip and in-group maneuvering has a long evolutionary history; it may have forced us to evolve. Next time you see a gossip mag, realize that this may be one of the reasons that we've gotten as smart as we have — weird thought.

The advantage of the 'social intelligence' theory of brain growth is that, because it's an intraspecific form of competition, or one amongst the members of a species, any individual's gain becomes a challenge to others. This kind of internal evolutionary arms race can drive rapid change because it keeps cranking up the pressure with each improvement.

If, at the same time, evolution loosened a constraint on a trait that's under this kind of pressure — like fixing limits on a big brain from diet and heat —you can get a pretty intense skewing of the trait through directional selection. This is the kind of pressure and release from constraint that together might produce a big spike in a metabolically expensive trait.

Relaxed limit, plus internal competition, plus big external pay-off can make for a real evolutionary upheaval.

Another possibility that some theorists have raised as an explanation for our brain is sexual selection: could women have preferred more intelligent mates, and their preference driven our ancestors' cognitive explosion? Well, it's possible, and the argument is not really opposed to the social intelligence thesis. The two could have worked together.

But what would we expect if sexual competition among men was the dynamic driving our increasing intelligence? Well, we would probably expect sexual dimorphism; men's brains could get much better developed than women's, like a peacock's tail or a silverback gorilla's enormous muscles.

That's not really what we find, though. Men and women are quite close in brain size, when you take into account the difference in their body size. There are subtle differences between men's and women's brains, but nowhere near what you'd expect in a trait driven by mate choice, especially a trait that's undergoing such intense selective pressure that it's changed radically in a few million years.

But the reason that I think it's still worth considering sexual selection is this: ask yourself, how would one of our female ancestors know which male was more intelligent? She would have to be intelligent too, especially if some of the less-bright hominid males were trying to fake it. If some of our male ancestors were trying to fake being brighter than they really were, you'd have created a selective advantage for smarter women.

If that's the case, you might wind up with symmetrical sexual selection, mate choice driving both the chosen and the chooser to evolve more and more intelligence, putting pressure on both men and women.

I suspect that these forces were working in conjunction: our ancestors' increasingly sophisticated strategies for getting and preparing food, changing ecology and technology, social competition, alliances and deception, and even sexual selection for intelligence, among men and women.

Ratcheting up intelligence

Why did out ancestors' get bigger so much faster though, if all these selective forces were there before?

One possibility is that about two million years ago, there was a real shift in the way that these pressures interacted which caused the spike in growth. The idea is that, at a certain point, our ancestors became so capable of getting food, protecting themselves from predators, and shielding themselves from the environment that they achieved a kind of 'ecological dominance.' Once external selective forces were relaxed, sexual selection and social competition could exercise greater influence on brain development.

The problem for our ancestors is that, with 'ecological dominance,' the population of humans started to increase. At first the excess population spread to new territory, especially because meat-eaters need a bigger range than vegetarians. But, eventually, our ancestors' own success started to bite; the crowding ramped up pressure on each other.

First, it drove them out of Africa, as they followed the animals that they hunted. Later on, much later on — about 15,000 years ago — the increased population would start to really prove a problem, when our ancestors suffered through another brief ice age that dried out the planet. This made it harder and harder to find the foods that they had learned to eat. Our ancestors' success, their growing numbers, would eventually lead to the slow dawn of agriculture, then to the domestication of animals.

Most anthropologists don't think that our ancestors figured out agriculture because they just thought it was a great idea. We think they were forced into it. Their own success at getting food and growing their numbers, even setting up permanent places to live, would become a burden when the climate changed. During one of these bottlenecks, some of them would start to figure out how to help the environment to provide them with more food.

In the Middle East, and elsewhere, our human ancestors started to learn how to manipulate that environment, so that it provided more food. They started to change the way water flowed, used fire to shift the types of plants in the forest, hunted more carefully and entered a new kind of relationship with nature, where nature itself was changed. We don't know exactly when it started, and it probably wasn't totally conscious when it did start, but when humans started to modify the environment they accelerated the processes of niche creation.

But that social crowding may have also produced a new kind of relation, an intensification of human communication. We don't know when language started, but once humans had it, they began to pass on to their children how they saw the world in a new and more powerful way.

Language demonstrates clearly that the accomplishments of human intelligence are not simply the product of the human brain alone, in isolation. No one invents his or her own language. We are born immersed in an environment in which language is a constant presence, and we gradually take it on board. Adults help us along the way, simplifying how they talk to us, pointing things out, correcting us, providing role models of how to use language.

Our brains, including those hyper-social instincts, like paying super close attention to other people, make us really good at imitating compared to other primates, but our environments help us along. If you show a child and a chimpanzee how to use a tool to do something like get a treat, they can both learn how to use the tool.

But if you show them both how to use it with a strange and inefficient technique, the chimp will probably just play with the tool until it finds a way — most likely a better way — to get what it wants. The human child, on the other hand, will copy your technique, usually with excellent fidelity, even though your technique is lousy. Human social skills are stronger than our own ability to problem solve as children.

In the process of social learning, then, you inherent with language a way of seeing the world, with all sorts of cognitive skills and information embedded in it, but also biases and blindspots. We benefit from the accumulated knowledge and skill of our ancestors, just as we benefit from the way that they have changed the environment: eliminating predators, building up permanent shelter, exploring the places we live and finding the resources. Niche creation is environmental, but it's also cognitive; we create a niche to grow a human brain around the infant.

Add together increased population density, excellent transmission of information, and language you have a really strong channel for inheriting knowledge. Less gets lost each generation.

Most chimpanzee culture and technology can basically be re-invented in a generation. It's not cumulative. You don't need to figure out how to make one tool, to make another tool, to make another tool. Human culture, in contrast, is the result of many generations of transmission and gradual improvement; you couldn't re-invent it by yourself, alone, no matter how smart you were. The point is, to truly understand how humans have evolved to become so peculiar, you have to recognize that our social skills are as important as our brains because our social skills allow our brains to work together over generation upon generation.

Michael Tomasello, a psychologist and evolutionary theorist, has called this the 'ratchet effect.'

A ratchet wrench is a wrench that can only turn one way; as you tighten a bolt, you move it freely one way and the other, but it only twists the bolt in the direction you want it to go. It doesn't twist backward; you can't lose progress.

Culture and technology develop a 'ratchet' when innovations don't get lost. If an individual has an insight or makes an invention, social ties preserve that information so that the innovation will not die with the inventor. At that stage, technology only goes in one direction.

The ratchet takes a while in human evolution to get going. At first, we have the information getting transferred successfully, but the tools remained the same for a very, very long time — a million years, really. But eventually, when we start to increase the intelligence, add in a bit more creativity, improve the problem solving, and multiply the number of potential improvers who are communicating, the cultural ratchet starts to turn — at first slowly — click, click, click.

For example, when I show students how our tools changed, I think that they're underwhelmed; some of the most sophisticated stone tools, the last to develop, are the microliths. These are tiny stone tools, often glued with tree resin into wood handles or used for very specialized purposes. But these tools were the sign of a truly diverse, innovative tool kit.

Special tools for hunting big game, special tools for fishing, special tools for catching birds, digging up roots, making clothing, preparing skin, cutting down grass — harpoons and fish hooks and needles and saws with teeth — tons of techniques and bits of advice that have to get passed down from parent to child. They're a sign of that ratchet — click, click — new inventions, modifications and improvements on old tools. Now, we've got something that looks like human culture.

Probably with the development of *Homo erectus*, we began to have a kind of bio-cultural evolution, but it would really take off with modern humans in the last 200,000 years. Learning would be absolutely essential to survival, and the demands of culture — making tools, finding food, fashioning shelter, maybe even making fire and cooking — would have become a selective pressure on our brains. These skills demanded intelligence and ability, but they also demanded intense social skills — learning, imitating, teaching, cooperating, even specializing within a group.

You've got a fully human mind at this point, but you also see that our intelligence is not just determined by what's encased in our skulls. We inherit so much from our ancestors because we have the cognitive, social and organizational skills to take it on board. We have to be immature when we're born because we have so much to absorb after we get here.

The funny thing is, the social nature of our intelligence is our great advantage, but it's also our Achilles' heel. We don't just get correct ideas or accurate insights. Sometimes we absorb mistakes, biased perceptions, or obsolete patterns of thinking. Yes, we stand on the shoulders of our ancestors, so we can see further. But we also have to realize that we sometimes see through their eyes, even when they didn't perceive things clearly.

The end of evolution?

So, that's how evolution made us. We've blown past some details, rushed past some great debates, and left out a lot of unanswered questions, but the last four weeks have been the basics of how humans have evolved.

You might asking, What next? Is evolution over? Surely, natural selection can't be able to get to us, protected as we are with our advanced medicine, our hygiene, and our sophisticated technology. I mean, it's not like there's bears prowling the streets, picking off the weak and slow, right?

For a long time, anthropologists thought human evolution was over, or at least that we had fundamentally changed the dynamics. We were so convinced that technology and culture buffered us against selection that many theorists came to the conclusion that the biological chapter of our history was already written. If we were to evolve any further, they thought, our technology, culture, or overall enlightenment would be the avenue.

Well, the genetic evidence has come back, and it's pretty clear that selection is not done with us. In fact, by most genetic measures, the past 20,000 years or so may have been some of the most rapid evolution in our species' history, with all sorts of selective pressures on our genome. Preliminary results suggest that pressure especially seems to be on genes linked to our immune system, brain function, metabolism and digestion.

Turns out that the only time a species stops evolving is when it's extinct, and we're not dead yet.

If you think about it more deeply, it makes sense. If evolution is variation, inheritance, and selection over time leading to adaptation — VISTA — the basic factors are all still in place. There's no reason to think they've stopped, is there?

First, we've got more variation than ever before. There's over seven billion of us on Earth today, having a lot of babies; that's up from two billion less than a century ago, and only 5 million back in 9000 BC. Population increased 1000 times!

The expansion of our species around the globe and the growing size of the population have already produced some interesting quirks. Anthropologist John Hawks points out that ten thousand years ago, no one on the planet had blue eyes; that gene has developed recently, meaning that only 400 generations has produced a noticeable change.

In fact, the rate of mutation may actually be going up because older fathers tend to have more mutations in their sperm. In some countries, the average age of fathers has increased dramatically, suggesting that we might be producing more genetic innovation than before.

Inheritance hasn't changed. We may know what's going on, and in some of the wealthier countries, we're doing genetic counseling for couples at risk of having babies with certain birth defects. But we haven't replaced sexual reproduction and recombination with cloning or cryogenic freezing, and it's not clear that we will anytime in the near future.

But, aha, you say, surely there's no selection going on? After all, everyone survives to reproduce, if they want to, don't they...?

Actually, selection is going on. You just have to know where to look for it.

First, any time there's a radical change in the environment, you'd expect that selective pressures would also shift quickly, tossing any existing stabilizing selection and equilibrium out the window. No one can doubt that our environment right now is in a state of flux. The only question is how much change and what kind.

Right now, for example, the forces of erosion are only moving around one-tenth the amount of soil that humans are moving around. Researchers in the US estimate that 30 tons of earth get moved for every individual. We're changing the amount of heavy metals in the atmosphere, dumping waste products at an unprecedented pace — over one billion tons last year — and some of this waste has no foreseeable way to decompose before it's going to wind up in the food chain.

Most biologists are of the opinion that we are producing a sixth great extinction event on the planet. The first five wiped out at least half of all the species alive at the time, and it probably takes at least 10 million years for diversity to recover, as new species emerge out of the survivors.

Species go extinct all the time, it's true. That's the way evolution works. It's normal. But right now, the extinction rate appears to be way above normal. Scientists estimate that 40% of the species may be in danger of dying out in the near future. The rate is at least 100 times higher than normal; the famous biologist E. O. Wilson has argued that the actual rate is probably 1000, even 10,000 times above what is normal. Humans are having an impact similar to the meteor strike that wiped out the dinosaurs 65 million years ago.

You'd have to be pretty confident about our situation as a species if you looked around and said, yeah, all those other animals are evolving or going extinct, but nothing's happening to us.

You'd also have to be pretty oblivious to the way that most of us in the world today live.

Last year, 7 million children under the age of five died; that's around 5% of all the children in that age bracket. That number is down a lot from what it was even fifteen years ago, which is great, but there are parts of the world right now, countries like Afghanistan, Mali, and Somalia, where infant mortality gets as high as 10% before a child's first birthday. I'm not even got to talk about this from a human right's perspective; from an evolutionary perspective, it should certainly put to rest the idea that our species has universally escaped from selective pressures. We've made huge strides in global health, but pneumonia, malaria and diarrhea are still working their way through some parts of our gene pool, viciously weeding out those who are particularly susceptible.

Some evolutionary theorists are discussing the possibility that humans will have to evolve resistance to HIV, probably in those places where infection rates are the highest. We know that some people are particularly resistant to developing full-blown AIDS from the virus, and there's lots of evidence that chimpanzees had to do something similar a few million years ago; their genome is littered with retroviral DNA from an attack by a similar disease.

We've done a great job of getting rid of some selective pressures. And it's not just bears. But it turns out that living close together was a really rough transition for humans that subjected us to a whole new set of pressures. For most of its history, London has been a population sink; more people have died there than been born, the countryside supplying a steady stream of immigrants to reinforce the population. When Darwin was writing *On the Origin of Species*, infant mortality may have been as high as 50% in England.

And those cities bred some pretty amazing diseases; just ask the Native Americans. When Columbus and the rest of the crew from Spain, Portugal, England and the other maritime powers showed up in the Americas, they brought with them diseases that had evolved in the streets and slaughterhouses and sewers of European cities. The Europeans had developed resistance over centuries of suffering from plagues and epidemics; the Americans had no resistance. In some cases, the mortality rate following colonization was over 90%, people dying, not just from disease, but from over-work, war, and the complete collapse of all their social structures.

Talk about a bottleneck even for genetic diversity in the Americas! It may seem like ancient history to us, with a world that seems to change every decade, but in an evolutionary framework, a few dozen generations isn't much time at all. We're in a super-heated phase of evolution.

Where to from here?

When we look around, if we live in wealthy countries, sure, we can be forgiven for thinking that the laws of natural selection have been repealed. In some rich countries, we've done a great job on infant morality. In parts of the industrialized world, it has dropped below 1%. That's a huge accomplishment. Absolutely, in these pockets of human population, the selective pressures of pneumonia, malaria, tuberculosis, and other killers of children have been held at bay.

But even the way that we've abolished certain diseases and malnutrition may be rebounding back around to create new selective pressures on those people —¬†and don't forget, relaxing the pressure on one part of the gene pool doesn't mean it's been abolished for the whole of the species, by any stretch.

For example, as many of you probably know, our widespread use of antibiotics to keep us safe, even to keep our domestic animals safe, is starting to really scare some epidemiologists. We've created a tough world to be an infectious bacteria. But that means that some of the strongest are surviving, adapting, and getting harder to kill. Our growing population, more and more densely packed cities, and all the crowded agriculture facilities where we raise our food, may also be breeding the next major selective event in our own stockyards or hospitals.

Among the wealthiest people, we've abolished malnutrition as a selective pressure, for certain, but we've also placed ourselves under pressure to adapt to a rapidly changing diet. People may not starve today in some places because of agriculture, but agriculture makes demands on our bodies, including adapting to a shift in the type of food and the profile of nutrients we get. The evidence from genetic research is that our ability to process food is under intense selective pressure; remember, 10,000 years ago, virtually no adult humans could digest milk.

We're also staring down the barrel of an obesity epidemic in some parts of the world, a reminder of how our bodies have not all successfully adapted to our changing way of life. We know that obesity affects fertility in both men and women. Fat produces estrogen, so obese men have lower levels of androgens and can even wind up with erectile dysfunction. Obesity in women can mess with their reproductive cycle, even leading to amenorrhea, or the interruption of the menstrual cycle.

We suspect that male sperm count has dropped in recent years. Boys alive today tend to have lower sperm counts than their grandfathers' generation, although this varies a lot from one to the next, and it may be affected by changes in the way we measure the count. However, if a French research team that studied data from more than 100 fertility clinics is correct, the average sperm count may be dropping by 2% a year there. We don't know for sure why — some reproductive scientists worry it's synthetic chemicals that mimic hormones in our bodies — but the European Science Foundation report that one in five young men had a 'sub-fertile' sperm count.

If it's happening — and this is controversial — some individuals may be more resilient, meaning that they have a trait that will likely be selected for by reproductive success.

Remember, it’s the population as a whole and not any single individual we’re more concerned about, so there will be lots of exceptions even if the trend is very clear across the whole group.

My goal is not to scare people about their weight or their sperm counts or anything else. The point is that, given our changed, unprecedented nutritional, chemical, and technological environments, there’s whole new forces shaping our reproductive success. Depending upon how your body responds to the new environment, you may be more or less successful at surviving and reproducing. We may not be able to see it happening because, even though the pace of evolutionary change has accelerated, no one is going to change in front of your eyes. The shift will be slow, from one generation to the next, almost, almost imperceptible.

However, recently in the UK, some researchers may have caught it. Using widespread surveys of health and basic measurements, the researchers found that UK women were becoming shorter, stouter, with lower cholesterol levels, lower blood pressure, and extended windows of fertility. We can’t tell on such a short time scale, but these women may be, as a group, adapting to our radically changing environment.

All of these changes punch huge holes in any simple distinction between natural selection and artificial or ‘human-driven’ processes. We are having such a massive impact on our environment, doing so much niche creation, changing our way of life so much, that it’s really hard to argue that anything around us is ‘natural’ anymore. We may think of ‘nature’ as flowers and birds and forests, but right now, for the purposes of natural selection, it’s everything around you that affects your survival or your ability to reproduce.

This doesn’t mean we’re doing anything intentional to make ourselves evolve. I’m kind of suspicious of anyone who says that they think we’re going to be able to plan our future evolution. In fact, most of us have no idea how we are changing the selective forces that are shaping us. In addition, we’re probably not even used to thinking of evolution this way — many of us are more used to getting excited about technology when we think about our future, not the way that this technology might affect our reproductive success.

There’s really no way to know what is going to happen. Or, as the great philosopher Yogi Berra, warned: ‘It's tough to make predictions, especially about the future.’

In spite of the difficulty of predicting the future, however, I want you to think about it. And I want to leave you with the words of Jonas Salk, the discoverer of the polio vaccine, and a man who refused to patent the discovery because he thought it was better for the good of humankind. Salk was of the opinion that:

‘The most meaningful activity in which a human can be engaged is one that is directly related to human evolution. This is true because human beings now play an active and critical role not only in the process of their own evolution but in the survival and evolution of all living beings. Awareness of this places upon human beings a responsibility for their participation in and contribution to the process of evolution.’

Evolution shows how we were all stitched together at the start: all humans, all living things, arisen from shared ancestors. But it also shows how we are tied together in the future. What we do now affects how other life will evolve, whether some forms of it will disappear. But it also affects our descendants, and whether they would recognize us, or prefer not to know about us.

References & Resources

Key concepts

Human brain evolution is unusual, especially the degree of encephalisation, requiring us to think about how such a metabolically expensive organ could be 'afforded' by our ancestors.

Brain function tends to involve repurposing of old brain areas and layering new types of control, even over automatic functions.

Human intelligence is not just the result of a large brain, but also a modified social life and developmental trajectory that encourages learning.

Genetic and other evidence suggests human evolution is not over; natural selection is liable to remain an important process in human genetic change.

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Figure 1

The coccyx, from Gray's Anatomy. Image in the Public Domain.
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Figure 2

Cross-section of embryonic tail. Source: (Modified from plate 22 of Fallon and Simandl 1978). http://www.talkorigins.org/faqs/comdesc/section2.html

Figure 3

X-ray image of an atavistic tail found in a six-year old girl. Source: reproduced from Bar-Maor et al. 1980, Figure 3. http://www.talkorigins.org/faqs/comdesc/section2.html

Figure 4

Louis, trusty dog, photo by Greg Downey, Creative Commons (BY NC).

Figure 5

Homologies, image by Vladislav Petrovich Volkov, 2011, released into the public domain.

Figure 6

Jeffrey, absurdly charismatic Shetland Pony, photo by Greg Downey, Creative Commons (BY NC).

Figure 7

Tetrapod forelimbs, image by Wilhelm Leche, 1909. Public domain.

Figure 8

Convergent structure in analogous wings, diagram by John Romanes (1892): Darwin and after Darwin, Public domain. Source: http://commons.wikimedia.org/wiki/File:Homology.jpg

Figure 9

Drawing from Charles Darwin's *First Notebook on Transmutation of Species* (1837) Public domain. Original location: http://commons.wikimedia.org/wiki/File:Darwins_first_tree.jpg

Glossary

Acheulean

(Sometimes 'Acheulian') Derived from the name Saint-Acheul, a suburb of Amiens in France. These tools are also sometimes referred to as 'Mode 2' technology.

First developed around 1.8 million years ago, Acheulean stone tools are associated first with the rise of *Homo erectus*/*Homo ergaster*. These tools tend to be more thoroughly worked, on all sides, unlike earlier Olduwan tools. The distinctive teardrop-shaped Acheulean hand-axe, a symmetrical tool, is found over a wide geographic range.

Related Terms: Olduwan

Adaptive radiation

A pattern of diversifying or disruptive evolutionary change, leading from a single species into multiple different species over time, with each adapted to a different niche. The rise of multiple different specialised mammal species from one or a small number of mammals into thousands is often cited as an example of adaptive radiation.

Related Terms: Diversifying selection, Homologies

Allele

One of the variants that can occur at a particular gene or genetic locus in a cell's DNA. In some cases, an allele will produce an actual observable difference in an organism's phenotype or traits, but in others, an allele will not produce an expressed difference.

Related Terms: Continuous, Discreet, DNA, Dominant gene, Recessive

Alloparenting

A pattern of multi-individual parenting or assistance to a mother in raising offspring, from either unrelated individuals or individuals related to the child (e.g., siblings, father, parents' siblings like aunts, grandparent... etc.). Alloparenting distributes the demands of altricial human infants and can thus lead to shorter birth spacing and greater fertility for women.

Related Terms: Birth spacing

Altricial

An individual who requires great assistance, especially an infant who is particularly helpless and unable to care for her- or himself. Humans are very altricial relative to other more 'precocial' (or self-sufficient at an early age) species' infants.

Related Terms: Metabolic ceiling, Obstetrical dilemma, Precocial, Sexual revolution

Anisogamy

Anisogamy is sexual reproduction between two sexes who do not contribute similar gametes. The smaller gamete, referred to as the sperm, determines which sex is male; the female contributes the larger gamete, or egg.

Related Terms: Sex

Anthropocentric

A tendency to see humanity as the most important topic of biological research and even to over-ephasise the importance of humanity. Anthropocentric theories often fail to recognise how unusual humans are or the complexity of non-human life.

Related Terms: Great Chain of Being, Teleological error

Atavism

A trait in an individual that does not appear in its parents or immediate ancestors, but was present in a much older ancestor. A recurrence of an ancient trait that no longer manifests in other contemporary members of a species. In laymans' terms, an evolutionary 'throwback' of a trait to an earlier variant.

Related Terms: Vestigial organ

Birth spacing

The interval between births, often affected by breast-feeding (feeding on-demand can suppress fertility), maternal body weight and exercise levels, and overall fertility. Humans have shorter birth-spacing intervals than some of the other apes, like orangutans, leading to higher fertility in our species. Some credit our relatively shortened birth spacing to alloparenting.

Related Terms: Alloparenting

Bodily cells

The cells of the body, opposed to germ cells, which are the reproductive cells (and thus the first cells of your future offspring's body). According to Weismann, body cells could adapt or be affected by the environment, but any changes to bodily cells would not be passed on to offspring, because the communication between your germ cells and bodily cells was one-way only.

Related Terms: Germ cells, Weismann barrier

Bonobo

Pan bonobo. The less common species of chimpanzee. Only discovered by Western scientists in the twentieth century. Although physically similar to common chimpanzees (*Pan paniscus*), bonobos have distinctive patterns of social interaction.

Brain stem

In vertebrate neural anatomy the brain stem (or brainstem) is the rear part of the brain, connected to and structurally continuous with the spinal cord. The brain stem communicates be- tween the rest of the brain and the nervous system and provides regulation of some automatic functions, like cardiac rhythm and breathing.

Broca's area

Broca's area is a region of the hominid brain cortex in the left hemisphere linked to speech production. The area is named for French neurosurgeon Paul Broca, who discovered its function while examining the brains of patients with brain injuries and language difficulties. The area is on the surface of the brain, right above the left ear.

Related Terms: Wernicke's area

Capoeira

An Afro-Brazilian martial art and dance, involving a distinctive musical style and vigorous, acrobatic movement. Greg studied capoeira in Brazil while working on his doctorate degree in order to understand how culture affected physical and psychological development of the people who practiced it.

Chimera

A chimera is an organism composed of two or more genetically distinctive populations of cells. Chimeras can be formed through the fusion of two initially separate fertilised eggs. Some cases of chimera have been reported in humans. Unlike a hybrid, in a chimera, the origin of each cell can be clearly determined as the two types are clearly distinct. Chimeras can also be created artificially; in some cases, biologists have placed foreign cells into an organism and these cells are assimilated into the animal's functional architecture.

Chloroplasts

Organelles found in plant cells and some other eukaryotic organisms. They are the parts of the plant cell responsible for photosynthesis, converting energy from sunlight into stored molecular energy.

Related Terms: Endosymbiotic theory, Photosynthesis, Symbiogenesis

Chordates

The phylum of animals which has a notochord, or a form of central nervous system. Vertebrates are a subphylum of the chordates, which also includes some animals, like the sea squirt, that have a notochord for part of their lives, but do not have a permanent central nervous system or vertebrae.

Coccyx

The ‘tail bone,’ or the final three to five spinal vertebrae, below the pelvis, that fuse into a single bone in primates without tails.

Cognitive niche

A concept proposed by John Tooby and Irven DeVore to explain human distinctiveness. According to these theorists, humans exploit an ecological and evolutionary niche made available by their cognitive skills. The concept of the ‘cognitive niche’ also can be linked to the idea of niche construction -- see glossary -- to capture the way that individuals are born into a personal environmental setting or niche where these distinctive cognitive skills are encouraged and developed.

Related Terms: Niche creation (or niche construction), Ratchet effect

Competitive exclusion

Sometimes referred to as Gause's law of competitive exclusion. The ecological principle that two species cannot compete stably for the same resources. One species will likely have an advantage, however slight, leading this species to dominate in the long term. The other competitor will either become extinct or be forced into a different ecological niche.

Related Terms: Interspecific competition

Concealed estrus

The lack of signaling in the females of a species when they are ovulating and fertile or ‘in heat.’ Unlike chimpanzees, who signal when they are fecund with genital swelling, human women offer no signal detectable to men when they are fertile. Gorillas are semi-concealed, suggesting that both chimpanzees and humans have evolved derived traits, or adapted with their own distinctive patterns since they shared a last common ancestor.

Related Terms: Estrus, Sexual revolution

Conserved

A conserved trait is stable over evolutionary time, or shared between descendants of a common ancestor. Often, conserved traits are believed to be important for survival, so they cannot vary without decreasing an organism’s chance of survival. Some traits or genes are highly conserved across multiple different species, owing to their essential role in organism functioning.

Related Terms: Hox genes

Continuous

A trait that varies with a smooth distribution and many intervening variants. For example, human skin colour and height are both continuous traits, with various individuals distributed across the whole range of possible phenotypes. Continuous traits tend to be determined by multiple genes (polygenic) rather than a single, discrete allele, which is more likely to produce a discreet trait.

Related Terms: Allele, Discreet, Polygenic

Convergent evolution

The evolution of similar features in organisms from distinct lineages. The example used in the text to explain convergent evolution is the wing: wings have developed in a range of species from different lineages (insects, pterosaurs, birds, and bats). Convergent traits often have quite distinct underlying structures, but the demands of the environment can shape them to have similar features. For example, wings are anatomically varied, but they all have certain shared traits because of the demands of flight: large surface area, flexibility, strong mechanisms for moving them, light weight.

Related Terms: Homologies

Copy number variation

A structural variation in the genome caused by an unusual number of copies of a section of the DNA sequence. A section may be copied an extra time, or missing. The human genome contains a large number of these duplicate areas; sometimes identical twins vary in the number of copies that they have of a section of DNA.

Related Terms: ‘Junk’ DNA, Mutation

Cyanobacteria

Also called ‘blue-green algae,’ cyanobacteria produce energy through photosynthesis. They take their name from their colour (‘cyano’ is from the Greek word for ‘blue’). Endosymbiotic theory holds that plants gained chloroplasts by capturing symbiotic forms of cyanobacteria. Cyanobacteria are also widely credited with oxygenating Earth’s atmosphere.

Related Terms: Chloroplast, Endosymbiotic theory, Photosynthesis

Diagonal transmission

A term used to describe transmission of traits from adults of a species to children who are not their own. That is, ‘diagonal’ transmission occurs when behaviour, traits or practices can be communicated to genetically unrelated young of the species, either through copying, teaching, or a mechanism like cognitive niche creation. Without diagonal transmission, traits are only inherited from one’s parent or parents.

Related Terms: Cognitive niche, Inheritance of acquired traits, Lateral transmission, Ratchet effect

Dimorphism

Phenotypic difference between the males and females of a species; that is, a ‘dimorphic’ species has two forms, one for each of the sexes. (Some species are polymorphic.) The greater the difference in the sexes, in some species, the clearer indication that individuals are engaged in sexual competition.

Related Terms: Direct competition, Sexual revolution, Sexual selection

Direct competition

A form of sexual selection in which members of one sex compete directly — through confrontation or ritualised combat. In elephant seals, for examples, males fight for control of breeding females, a process which has favoured the development of extremely large males (and thus increased sexual dimorphism).

Related Terms: Dimorphism, Sexual revolution, Sexual selection

Directional selection

A pattern of natural selection in which one variant of a species is favoured, leading a species to skew over time so that this variation becomes more and more predominant. Over time, directional selection can lead a species to adapt and change significantly.

Related Terms: Stabilising selection

Discreet

A discreet trait typically has two alternative expressions, with no or little intervening expression or what is sometimes called discontinuous expression. A trait like biological sex (male and female) is discontinuous, with any mixed expression extremely unusual. Discontinuous expression or discreet traits are typically understood to be the result of a trait determined by a single allele. Gregor Mendel first proposed genetic inheritance through his research on discreet traits in pea plants.

Related Terms: Allele, Continuous, Dominant gene, Recessive

Diversifying selection

A pattern of natural selection in which different parts of a population adapt in distinct ways, often leading to a disruptive pattern for key adaptive traits. For example, if a species exists across an ecological range with a variety of niches, members of the species may be subject to different selective pressures, leading to a variety of traits being selected. In extreme cases, diversifying selection can lead to speciation, especially if the different parts of the population are isolated from reproducing with each other, preventing gene flow.

Related Terms: Adaptive radiation, Speciation, Stabilising selection

DNA

Deoxyribonucleic acid (DNA) is a molecule that encodes the genetic instructions used in the development and functioning of all known living organisms, founding in the nucleus of cells. Genetic information is encoded as sequences of four nucleotides — guanine, adenine, thymine, and cytosine (frequently indicated by their initials: G, A, T, C). Most, though not all, living cells have their DNA as a kind of spiraling, wound up ladder shape, with two spine-like chains of sugar-phosphates molecules linked by ‘rungs’ of the nucleotides.

Related Terms: "Junk” DNA, Allele, Double helix, Epigenetics, mtDNA, Mutation

Dominant gene

With a discreet trait, one allele is dominant when it masks the presence of the other, recessive allele, in an organism’s phenotypic expression. An organism can carry the allele for the recessive trait without it being expressed if it occurs alongside the dominant allele.

Related Terms: Allele, Discreet, Particulate inheritance, Recessive

Double helix

The double helix is the structure of the DNA molecule in most, though not all, living things. The term describes the ladder-like structure of the nucleotide bases linking two sugar-phosphate chains in a spiraling structure.

Related Terms: DNA

Ecological dominance

Originally suggested by Richard Alexander, the theory of ecological dominance suggests that our hominin ancestors, at some point in evolutionary history, became so capable of resisting selective forces in nature — hunger, predators, climate — that intraspecific competition became disproportionately important in shaping human evolution. Whether or not our ancestors became ‘dominant,’ the theory draws attention to the important roles played by social competition, inter-group rivalry, and cooperation in human evolution.

Related Terms: Environmental theories, Intraspecific competition

Emotionally modern

Sarah Blaffer Hrdy has suggested that one of the key changes in human evolution is a shift in the motivational and emotional structure of our ancestors, diminishing within-group aggression, allowing suppression of instinctive responses, and allowing for greater cooperation. Her theory suggests that these changes may have preceded other cognitive changes — such as language or complex learning — laying the social and emotional foundation for sub- sequent cognitive shifts.

Related Terms: Social cognition

Encephalisation

The process over evolutionary time of species developing larger-than-expected brain size given their body weight. A precise measure of encephalisation is difficult, however, due to the allometric relationship between body size and brain size, and disagreement about how to measure relative encephalisation.

Related Terms: Expensive tissue

Endogenous

Refers to substances, processes or events that are initiated from within an organism or entity. In this book, endogenous viruses are viral sequences of DNA that are carried into the zygote with the germ cells, either the sperm or egg. In other words, endogenous substances are passed on from parent to offspring as a fact of reproduction.

Related Terms: Retrovirus

Endosymbiotic theory

First proposed by Russian botanist Konstantin Mereschkowski, endosymbiotic theory argues that some of the structures in complex living cells developed through evolution from symbiotic lifeforms that were originally separate. Later advocated most notably by Lynn Margulis, endosymbiotic theory proposes specifically that eukaryotic cells — the foundation of complex life — began as symbiotic communities of less complex structures. Most notably, the theory has been given support by the study of chloroplasts, mitochondria, and other organelles that contain their own sequences of DNA, shorter than nuclear DNA, and seem to go through their own forms of reproduction as cells reproduce.

Related Terms: Chloroplasts, Mitochondria, Symbiogenesis, Symbiosis

Environmental theories

Theories of evolutionary change that privilege external forces as shaping an organism. In the case of humans, especially the development of human encephalisation and cognitive elaboration, environmental theories suggest that the driving factors were the need to adapt to a variety of ecological niches, survive climactic change, forage for varied food sources, convert to a hunting-based diet, or contend with other external threats. Often contrasted with social theories of intelligence or accounts that focus on intraspecific competition.

Related Terms: Ecological dominance, Intraspecific competition, Machiavellian intelligence

Epigenetics

The study in genetics of changes in gene expression in phenotype that arise from non-genetic sources. Epigenetics investigates how functional changes can occur in the genome without changing the sequence of nucleotides, through such processes as DNA methylation and histone modification, both of which can lead to alterations in gene expression while leaving the underlying DNA sequence unchanged.

Related Terms: DNA, Hunger Winter, Inheritance of acquired traits, Weismann barrier

Estrogen

Also spelled, 'oestrogen' (primarily in UK). A group of compounds that are essential in moderating female reproduction and the menstrual cycle, found in vertebrates and insects. The widespread presence and conserved nature of estrogens across species suggests that these sex hormones have a deep evolutionary history and profound importance in reproduction and survival. Although at much higher levels at women, especially during child-bearing years, estrogens also appear in men, and are essential to normal body function.

Related Terms: Sex, Sex-determining region of the Y chromosome (SRY), Testosterone

Estrus

The phase in a female animal's menstrual cycle when she is fertile and sexually receptive (sometimes referred to popularly with horses and other domesticated animals as 'in heat'). In some species, estrus is accompanied by visible signals of receptivity, such as swollen or brightly coloured genitalia or by distinctive behaviour, such as the lordosis reflex, when receptive females present themselves for mounting to males. In humans, estrus is largely concealed, although some researchers argue that there are changes in female behaviour.

Related Terms: Concealed estrus

Eukaryotic cells

A eukaryote is an organism whose cells contain complex structures enclosed within membranes, especially a separated cell nucleus. In contrast, prokaryotes, including Bacteria and Archaea, do not have internal, membrane-enclosed structures. All multicellular organisms are eukarylotic, as well as many single-celled organisms.

Related Terms: Symbiogenesis

Eusocial

The most complex forms of social organisation in a species are eusocial, and they involve high degrees of specialisation, often including some members of a group who are non-reproductive. Bees, termites, wasps and ants are the clearest example of eusociality, with large numbers of sterile drones, workers or warriors supporting a much smaller group of individuals who specialise in reproduction, including a 'queen.' The evolutionary success of eusociality is explained in large part by inclusive fitness; even though sterile workers will not pass on their own genetic material, their cooperation is essential to the survival of closely-related, reproductively-specialised siblings who will.

Related Terms: Group selection

Exaptation

Also sometimes called a 'pre-adaptation,' an exaptation is a trait that shifts function over time, leading to successive cycles of modification. For example, feathers first arose on flight-less dinosaurs, likely to serve either in sexual selection or as insulation and thermal regulation. Only later were those feathers exapted to serve for flight. The process of exaptation can leave imperfectly adapted traits or structures that clearly evidence earlier functions. Al- though the concept preceded their discussion, Stephen Jay Gould and Elizabeth S. Vrba introduced the specific term, 'exaptation.'

Related Terms: Neural reuse or neural recycling

Expensive tissue

The "expensive tissue" hypothesis was first proposed by proposed by Leslie Aiello and Peter Wheeler in 1995. They proposed that our ancestors underwent an evolutionary trade-off between the size of the brain and that of the digestive tract, which is smaller than expected for a primate of our body size. Since both brains and digestive tract use more energy than other bodily tissues for their weight, Aiello and Wheeler proposed that our ancestors had to develop new techniques for getting calories because the ration between brain and gut-size had departed so much from what we find in other mammals.

In this book, I use the term "expensive tissue" more loosely, in part because the argument made by Aiello and Wheeler has come in for criticism. The fact that brain tissue is metabolically "expensive" is indisputable, and in most animals, this high metabolic "cost" (especially the need for energy) leads to a constraint on brain growth.

Related Terms: Encephalisation

Fitness

In evolutionary theory, the term 'fitness' describes an individual's or species' ability to survive and successfully reproduce. Over time, an organism's fitness is its ability to pass its genes on to the next generation. The popular understanding of 'fitness' as overall health or physical vitality is not the same, and can cause confusions in students of evolutionary theory.

Related Terms: Gene pool, Gene-level perspective, Inclusive fitness, VISTA

Gender

A range of behavioural, physical, and psychological traits which distinguish from masculinity from femininity. Social scientists and feminist scholars use the term 'gender' to distinguish social expectations and learned roles from biological differences linked to reproduction. In the course of their research, anthropologists and historians have found that gender norms — what is considered normal or acceptable for men and women — are subject to quite wide variation. Although sex and gender are linked and clearly affect each other, the process of socialization can often lead people to mistake gender traits (learned social normals) for sexual traits (innate and unalterable products of physiological difference between men and women).

Related Terms: Norms, Sex

Gene pool

The total sum of genetic information and variation in a species at any given time. The gene pool is the underlying genetic material in any population, and evolution works over generations to alter this gene pool through processes like natural selection and genetic drift (relatively random changes in gene frequency due to differential reproduction, without clear selective pressure). The term highlights both that species are inherently varied, and that evolution operates, not on an individual's traits, but on the total gene pool of a population over time.

Related Terms: Fitness, Gene-level perspective, Population

Gene-level perspective

Essential to the modern synthesis in evolutionary theory, a gene-level perspective focuses on the evolutionary effects of natural selection, not on individual organisms, but on the frequency and variation of genes in a population. Taken to an extreme, a gene-level perspective can lead to the exclusion of other phenomena that shape evolution, and a treatment of the gene as the only unit of selection. But the approach is a powerful tool for modeling and making predictions about evolutionary processes, and it helps to explain why some genes replicate successfully even if they are detrimental to the well-being of an individual.

Related Terms: Fitness, Gene pool

Germ cells

Germ cells are those cells that give rise to gametes — the sperm and egg in sexually reproducing organisms. The germ line cells can give rise to new organisms, whereas somatic or bodily cells cannot. Genetic changes to germ line cells will be passed on to subsequent generations.

Related Terms: Bodily cells

Gestational diabetes

In some women who have not had diabetes previously, the blood glucose levels can become very high during pregnancy, especially during their last trimester. Medical specialists debate whether this should be considered a disorder, as the high glucose levels seem to be caused by the placenta interfering with the insulin receptors in the mother. The high blood glucose levels can lead to the infant be larger than normal for its developmental age, and to other complications.

Great Chain of Being

Originally from Greek philosophical thought, the Great Chain of Being was an understanding of all things being arranged in a strict hierarchical order, ordained by the divine, from God down through the angelic beings, celestial bodies, kings and nobility, normal humans, wild animals, domesticated animals, trees, all other plants, precious stones, precious metals, and other minerals. For medieval thinkers, human occupied a crucial place, poised between the divine and the earthly, with flesh that could die but, at the same time, immortal souls. This model of the 'ladder' of life was even adopted by the early natural historians, including Linnaeus, the creator of our system of classifying species. We can hear echoes of these ideas in some popular understandings of evolution.

Related Terms: Anthropocentric, Teleological error

Group selection

A set of controversial theories that natural selection can act, not just on an individual, a gene or a population, but on competing groups, if they are organised. Group selection is often part of multi-level selection theories, where selective processes are seen to be operating simultaneously on multiple different levels of organisation (the gene, organism, group, species). Group selection might help to explain why socially advantageous traits could arise — traits like altruism, empathy, willingness to sacrifice oneself — that clearly might undermine individual fitness. One alternative explanation is inclusive fitness.

Related Terms: Eusocial, Inclusive fitness

Hermaphrodites

A hermaphrodite possesses structural traits of the reproductive systems of both males and females. Most researchers now use ‘inter-sexed’ instead when talking about humans, as many individuals who have traits of both males and females do not have reproductive structures of both. That is, some inter-sexed individuals are not hermaphrodites, but rather have more ambiguously sexualised organs. In some species, hermaphrodism is normal, with either sequential change between sexes, or the possession of both sets of reproductive organs.

Related Terms: Sex, Sex-determining region of the Y chromosome (SRY)

Holistic

In anthropology, the term ‘holism’ is used to describe an approach that does not seek to isolate a single facet of existence — biological, cultural, economic, social, symbolic, etc. — but rather seeks to understand how the various dimensions of human life interact. In a research environment where specialisation is essential for training and other practicalities, holistic approaches can require a significant degree of cooperation among specialists. In a discussion of human evolution, a holistic approach seeks to take all available data to understand how humans evolved, assuming that no single cause or type of process will likely be able to explain all the changes.

Homeostasis

A system that works to maintain consistency over time, especially in response to changing conditions. Usually applied to living things, the concept of homeostasis points out that organisms must actively work to achieve consistency as both their internal state and external environment are subject to change. Various monitoring, control and feedback mechanisms help organisms to maintain homeostasis.

Homologies

Structural similarities underlying dissimilar traits that demonstrate that two organisms have descended from a common ancestor. The dissimilarity is often a sign of adaptive radiation, as one structure, over times, is shaped by different selective pressures into diverse homologous structures.

Related Terms: Adaptive radiation, Hox genes

Hox genes

Hox or homeobox genes are a group of related genes that control the body plan of the embryo along its axis, from top to bottom. Hox genes produce transcription factors which bind to other parts of an organism's DNA, encouraging or suppressing expression of other genes. Often referred to as 'control genes,' Hox genes designate which part of a body a cell is building, so defective Hox genes can lead to conditions like 'antennapedia', in which a defective signal leads to the growth of legs where antenna should be on an insect. Although Ho genes are fascinating for many reasons, we discuss them here to show two things: 1) the highly con- served deep structure of life, as Hox genes are quite similar across all bilateral forms of life (that is, life with two sides that mirror image each other); and 2) to show how regulation of genetic expression can lead to diverse structures growing from quite similar protein-coding sequences of species' DNA.

Related Terms: Conserved, Homologies

Hunger Winter

The 'Hunger Winter' (*Hongerwinter*) was a famine during the winter of 1944 to 1945 in the German-occupied parts of the Netherlands toward the end of World War II. Although relatively few died, due to the work of collective soup kitchens, millions of Dutch citizens suffered severe malnutrition, leading to long-term health consequences, even in the children whose mothers were carrying them during the famine.

Related Terms: Epigenetics

Inclusive fitness

Inclusive fitness is the recognition that an organism's 'fitness' is really all of its genes that get passed on to the next generation, even if those genes are carried by its siblings or siblings' offspring. As evolutionary theorist W. D. Hamilton argued, an individual might be more 'fit' by this measure if it acted on behalf of its closely-related kin, not just in pursuit of its own survival or that of its children. Hamilton suggested that inclusive fitness, also sometimes referred to as 'kin selection' when focusing only on close kin, might explain altruism, cooperation, and self-sacrifice. An animal might give off a warning signal, for example, when a predator approached, putting itself in greater danger, but potentially protecting its group, including its close kin.

Related Terms: Fitness, Group selection

Inheritance of acquired traits

Suggested by French naturalist Jean-Baptiste Lamarck, and for this reason often called 'Lamarckian evolution,' the inheritance of acquired traits is the idea that organisms pass on the adaptations that they have made during their lifetime to their offspring. Although severely criticised by proponents of the modern synthesis, some contemporary evolutionary theorists now argue that some forms of inheritance, including epigenetics and cultural transmission, may demonstrate Lamarckian properties.

Related Terms: Epigenetics, Lateral transmission, Weismann barrier

Interspecific competition

Competition in evolution between different species, often trying to exploit the same resource. The success of one species can generate greater stress on its competitor. In an extreme, inter-species competition leads to competitive exclusion, in which one species will become extinct. Traits like high reproductive rates can aid a species in inter-specific competition.

Related Terms: Competitive exclusion

Intraspecific competition

Competition within a species for resources, reproduction or survival. In this form of competition, one member's of a species success threatens other members of the same species. For example, sexual competition is a form of intraspecific competition, as members of one sex vie to reproduce at the expense of other members of the same group.

Related Terms: Ecological dominance, Environmental theories, Sexual selection, Trivers' hypothesis

"Junk" DNA

A popular name for non-coding DNA, or sequences of nucleotides on DNA that do not encode for a particular protein. When the human genome was first decoded, 98% of the DNA was found to be non-coding, and was initially referred to as 'junk DNA' in some reports, especially in the popular press. Subsequent research showed that this non-coding DNA often had important functions, including regulating the expression of the coding sections of DNA. Current estimates are that approximately 80% of the human genome serves some biological function for the organism, although much of this research remains to be done.

Related Terms: DNA

Kluge

Sometimes written, 'kludge.' A clumsy or awkward solution to a problem, such as a temporary, jury-rigged repair or hastily-made modification to a system. Contrasted with a 'de- signed' solution, in which forethought goes into the creation of a solution which is appropriate and well-designed for the purpose it serves. In evolutionary theory, a 'kluge' refers to the odd, inelegant ways that organisms have often adapted, including in traits like the skeletal adaptations humans have for walking bipedally.

Related Terms: Teleological error

Lateral transmission

'Inheritance' of traits within a generation, through mechanisms like imitation, learning, or — in some single-celled organisms — exchange of genetic material. In sexually-reproducing species, lateral transmission is a way in which non-parents influence the development of off- spring, especially through culturally learning.

Related Terms: Diagonal transmission, Inheritance of acquired traits, Ratchet effect

Machiavellian intelligence

Proposed by Frans de Waal in his book, *Chimpanzee Politics*, 'Machiavellian intelligence' is a type of political savvy or social cognition that allows an individual to be a successful actor in a social group, including building alliances, recognising deception, and scheming against rivals. An early version of a social intelligence theory, de Waal pointed out that the greater cognitive abilities of chimpanzees were used more for intraspecific competition than for control of the environment.

Related Terms: Environmental theories, Social cognition

Marsupials

A group of mammals, related to placental mammals, that carry their offspring, who are born quite early compared to other mammals, in a pouch. The absence of the placenta makes the growing marsupial embryo more vulnerable to the mother's immune system, forcing an earlier birth and a longer period of development in the mother's pouch. Marsupials and placental mammals split at least 140 million years ago, and most marsupials are found in the Southern Hemisphere, especially in South American and Australia, the latter of which has been especially isolated from the other continents.

Related Terms: Placenta, Placental mammals

Mate choice

A form of sexual selection in which one sex (usually the female in mammals and birds) chooses which male with whom to mate based upon some kind of display, such as an elaborate mating dance, brightly-coloured feathers, sophisticated nest, or other indirect means of competition. Mate choice can lead the preferred trait to become quite pronounced, for example, in the peacock's tail.

Related Terms: Sexual selection

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Melanin

A naturally-occurring pigment found widely in living things (although spiders, curiously, don't seem to have it). Melanin is responsible for human skin colour, varying from deep saturation in populations who have long resided near the equator to quite pale shades in populations closer to the poles. Melanin protects the skin against ultraviolet light but can make it hard for the body to metabolise vitamin D in low-light situations.

Related Terms: Pigmentation

Menstruation

The periodic discharge of blood and mucosal tissue in women from the uterus during their reproductive life, stretching from menarche (the onset of menstruation) through menopause. Not all mammals undergo menstruation; why human women do, and whether the blood loss has an adaptive function, are the subject of debate in anthropology.

Metabolic ceiling

Dunsworth and colleagues (2012) have argued that human babies are born extremely altricial, not because of the obstetrical dilemma or limits set by the size of the birth canal, but because of energetic constraints. According to these researchers, humans can only maintain a metabolic rate 2.1 times the basal metabolic rate, the ceiling for metabolic exertion. In other words, the human fetus is so energy hungry that a mother's body simply cannot feed it internally beyond our nine-month gestation period.

Related Terms: Altricial, Obstetrical dilemma

Microbiome

The total population of microbes that live in and on the human body, including all over the skin, in the mouth and sinuses, under the eyelids, and in the gastro-intestinal tract. Currently, research is ongoing to understand the functioning of this diverse microbial life — which outnumbers the cells that make up our body — including its roles in helping to maintain health and well-being.

Related Terms: Symbiosis

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Microliths

Extremely small stone tools that are an indication of some of the more sophisticated lithic technology or 'stone age' tools. Microliths — very small points or flakes of stone — were often used in projectile points, including arrowheads, and in the manufacture of composite tools, that is, tools made from multiple different substances, such as stone glued with resin to wood handles.

Mitochondria

Small, membrane-enclosed organelles within most eukaryotic cells that they generate most of the cell's supply of chemical energy. Mitochondria are in the cell's cytoplasm, outside the nucleus; their number varies depending upon the cell type. Mitochondria undergo their own processes of reproduction and have their own, circular chromosome, providing evidence for symbiogenesis and allowing mitochondrial DNA (mtDNA) to be used as a 'molecular clock' for estimating how long ago individuals or species have shared a common ancestor.

Related Terms: Endosymbiotic theory, mtDNA, Symbiogenesis

Mixed martial arts

A fight sport allowing competitors to use a wide range of techniques, including kick-boxing, wrestling, and other martial arts. Since the early 1990s, mixed martial arts have become one of the fastest-growing sports, both at the professional and at the participatory level, although the sport has sparked controversy because of its inherent violence and the perception that contestants might be in danger.

Modern synthesis

Christened by evolutionary theorist, Julian Huxley, the 'modern synthesis' was the attempt in the twentieth century to combine Darwinian theory of natural selection with emerging theory in population genetics. Prior to the modern synthesis in the 1930s and 1940s, some biologists thought that findings in genetics were inconsistent with Darwin's theories. Although there have been significant additions, the modern synthesis is still the foundation for modern evolutionary theory.

Modular intelligence

Modular intelligence operates over a narrowly-defined domain, or a particular type of function. Some animals are quite good at highly specialized cognitive tasks, but cannot use their perceptions or intellectual abilities in novel fashion. One approach to understanding human intelligence is to point out that humans, too, have modular forms of intelligence, even a large collection of special-purpose, innate cognitive tools. In contrast, other theories argue that human intelligence is more general purpose or that, although specialized, our cognitive tools are not innate, but learned.

Related Terms: Neural reuse or neural recycling

mtDNA

mtDNA is mitochondrial DNA, the small circular chromosome found in the mitochondria of our cells. mtDNA is distinctive from nuclear DNA in eukaryotic cells, providing some sup- port to the theory of symbiogenesis. mtDNA is also inherited only from your mother, so it can be used to estimate the relatedness of individuals (at least along this maternal line), as the mtDNA only changes through mutation.

Related Terms: DNA, Mitochondria, Symbiogenesis

Mutation

A mutation is a spontaneous change to the sequence of nucleotides in DNA. A mutation can occur because of damage to the DNA (such as from radiation), because of an error in transcription or gene copying, or because of an accidental deletion, reversal, or insertion of a part of a sequence of DNA. If a mutation occurs to a coding portion of the DNA, that is, to a section that carries a gene for a protein, most often that mutation is detrimental. In some cases, however, mutation may produce a genetic variation with a selective advantage.

Related Terms: DNA, Recombination, VISTA

Neotony

The preservation of juvenile traits for an extended period, or even into adulthood, by an organism. Neotony is one way that variation can be induced through changes in an organism’s developmental timing.

Neural reuse or neural recycling

The idea that novel human cognitive abilities make use of brain regions or circuits that were used in our ancestors for other purposes, potentially biasing how they perform. For example, neuroscientist Stanislas Dehaene has argued that learning to read requires 'recycling' regions of the brain used in other primates for small object recognition. The neural reuse theory is one way to explain novel brain capacities in a modular brain. Other theorists argue that neural reuse is just a subset of a larger pattern of exaptation found throughout evolutionary theory.

Related Terms: Exaptation, Modular intelligence

Neuroanthropology

The anthropological study of human brain functioning, including especially a consideration of the ways that human neurological traits underwrite human diversity, and how diverse cultural and developmental contexts affect brain functioning. In some cases, neuroanthropologists seek to use field research to test hypotheses generated by laboratory-based neurosciences.

Niche creation (or niche construction)

A concept used by some evolutionary theorists to explain non-genetic ways that organisms may pass on influences to their offspring, through modification of the environment. In some cases, organisms build nests or structures that create conditions that facilitate reproduction and infant development. In other cases, an organism's activity modifies the environment so that the selective pressures on future generations will change. In the case of humans, our ability to modify our niche has changed profoundly, especially since agriculture, and moreso with industrialisation.

Related Terms: Cognitive niche

Norms

Social norms are collective principles, sometimes not made explicit, about how people should behave or what they should believe. Although the processes of socialisation and enculturation tend to make norms appear inevitable, or at the very least logical, they can often differ significantly among groups. For example, in one group, the norms for childcare might appear negligent or even cruel in another group.

Related Terms: Gender

Obstetrical dilemma

The conflict posed by the narrowing of the human pelvis, due to its adaptation for bipedalism, and the growth of the human brain, leading to larger skulls in infants. These two processes lead to a conflict around the size of the birth canal and potentially have made child- birth more difficult for modern women than for our more ancient hominin ancestors. For a long time, anthropologists thought that the obstetrical dilemma explained the extremely altricial nature of human infants; they had to be born before their heads grew too large to pass through the birth canal. Increasingly, we are also realising that the metabolic demands of the growing fetus may pose a more serious limit on the length of gestation prior to birth.

Related Terms: Altricial, Metabolic ceiling

Olduwan

Sometimes spelled, 'Oldowan.' The oldest and simplest types of stone tools, sometimes called 'Mode 1,' are Olduwan tools, named for the Olduvai Gorge in Tanzania's Rift Valley region where the first examples were found. Olduwan tools are characterised by minimal working, usually along only one or two edges, and tend to vary with the type of material being used. The oldest examples of Olduwan tools are 2.6 million years old, but these were likely not the first tools; the evidence of tool use in other apes suggests that the last common ancestor may have already used simple tools made from perishable materials.

Related Terms: Acheulean

Parasite

A parasite is an organism that lives, in part, from a host, who does not gain a benefit from the relationship. Some parasites require a host for a stage of their life. Unlike symbiots, parasites tend to decrease the fitness of their host and, in extreme cases, may kill their host. Many parasites are quite specialised, living only in a particular host species, and have short life cycles so that the host's defenses cannot evolve resistance to the parasite.

Related Terms: Symbiosis

Parental investment

Any energy, resources, time or other cost from a parent in the production and care for one of its offspring. Theoretically, the minimal 'investment' would be the time and energy to copulate or produce sperm and egg, but in many species, the investment is much greater. Parental investment helps us to understand sexual selection because the sex that must invest more in reproduction acts as a limiting factor on the other sex in reproduction, possibly leading to competition among members of the lessor-investing sex. Parental investment also helps us to understand how evolution might produce 'high investment' reproductive strategies, if the result is a marked increase in survival or reproductive success for the offspring.

Related Terms: Sexual selection, Trivers' hypothesis

Parthenogenesis

Some species reproduce through parthenogenesis, a form of asexual reproduction in which the embryo is grown from an unfertilised egg. In some species, parthenogenesis produces a full clone of the mother, with eggs containing the full complement of the mother's chromosomes.

Particulate inheritance

Discovered by Gregor Mendel, the theory of particulate inheritance explains that traits are passed on to offspring through sexual reproduction, not by simply mixing the traits of the parents, but by passing on discrete particles or factors of inheritance. We now refer to these particles as 'genes.' Mendel recognised that, even if a particle was not being expressed (that is, was not shaping an organism's appearance), it might still be passed on, only to reappear in the appearance of later offspring.

Related Terms: Dominant gene, Recessive

Permian-Triassic extinction

The largest extinction event yet on Earth, around 252 million years ago. Although scientists disagree about the finer details, including the timing, rapidness, whether the event was a single one or multiple 'pulses' of extinction, and the causes, evidence does suggest that severe climate change was involved. The extinction event may have been the result of a combination of forces, including a major asteroid impact, a period of increased volcanic activity, or the release of stored chemicals in the Earth's crust. The most severe extinction occurred in the oceans, as chemical changes in the atmosphere led to increased levels of carbon dioxide and decreased oxygen.

Photosynthesis

The process used by plants and other photosynthetic life to create chemical energy from light, building carbohydrates like sugars from combining carbon-dioxide and water. In plants, photosynthesis usually happens through a green pigment called chlorophyl in the chloroplasts in the plant cells.

Related Terms: Chloroplasts

Pigmentation

Human skin pigmentation or colouration is provided by different types of melanin, a naturally-occurring dye. Human skin pigmentation mostly likely became darker as our ancestors' body hair decreased and became finer than other apes as the colour provided protection from equatorial sun. In contrast, other apes have light-coloured skin under their fur (al- though their faces and hands can also be quite dark).

Related Terms: Melanin

Placenta

A structure in the uterus that connects the growing embryo to the mother's body. Nutrients and oxygen pass through the placenta to the embryo, and waste products are removed from the baby's body through the placenta. The human placenta is particularly 'invasive,' penetrating more deeply into the mother's endometrium, rerouting some of her arterial blood flow, than happens in some other mammals.

Related Terms: Marsupials, Placental mammals

Placental mammals

One of the two major branches of the mammalian family; the other is composed mostly of the marsupials. Some other animals, including some reptiles, have structures that resemble placentas, but a 'true' placenta is one of hallmarks of placental mammals.

Related Terms: Marsupials, Placenta

Polyandry

A relationship in which a single female mates with multiple males. In some human societies, marital relationships can be polyandrous, with women taking more than one husband, in some cases, marrying brothers. Polyandry is one form of the more general phenomenon: polygamy, or systems in which individuals can take multiple spouses.

Related Terms: Polygyny

Polygenic

A polygenic trait is controlled by two or more genes. In some cases, a large number of genes can affect a trait, and those genes can themselves be pleiotropic, affecting multiple traits. The point is that the folk understanding of genes — for example, that for every trait there is one and only one gene — can often be markedly different from the way the genome actually functions. Polygenic traits are often continuous, rather than discreet.

Related Terms: Continuous

Polygyny

Polygyny is a system of mating or marriage in which a single male individual takes multiple female mates or wives. Polygyny is a more specific term than ‘polygamy,’ which includes both polygyny and polyandry. Polygyny in animals can often lead to direct competition among males as a dominant male may seek to monopolise a number of females, preventing rivals from mating with them.

Related Terms: Polyandry

Population

A population is group or whole species, including all living members. We use the term in anthropology to focus our attention on the group as a whole, including its internal variation and even unexpressed genetic traits. As individuals are born, grow, reproduce and eventually die, the population as a whole evolves, with traits that are selected for becoming more pervasive and traits that are being selected against decreasing in frequency or even disappearing.

Related Terms: Gene pool

Precocial

An adjective used to describe infants that are neurologically and behaviourally mature, especially that are able to achieve some degree of self-sufficiency or ability to participate in a group similar to an adult at an early stage. Precocial infants, like horses, cows and sheep, al- though small at birth, are often able to keep up with adult members of their species quite quickly.

Related Terms: Altricial

Pro-social

An adjective that describes the extreme social nature, including cooperation and social intelligence, in some species that cannot simply be explained as the pursuit of one’s own self interest. Some anthropologists argue that ‘pro-social’ traits are not strictly beneficial — that is, a pro-social animal may be more empathetic or altruistic than strictly advantageous for its own survival and reproduction — because the overall payoff in terms of selective advantage outweighs the individual cost of altruistic acts.

Pseudogenes

Pseudogenes resemble genes that code for proteins, but they have accumulated enough mutations that they no longer function to produce those proteins. Pseudogenes are sometimes taken as evidence that the protein for which they coded is no longer necessary for the species' survival nor sufficiently advantageous to prevent the transmission and spread of the now-dysfunctional version of the gene (because of gene duplication, some pseudogenes are former extra copies of still-functioning genes). Although they do not code for proteins, pseudogenes sometimes serve other functions or affect the functioning of other genes.

Punctuated equilibrium

Punctuated equilibrium is an evolutionary model suggesting that, over time, species can re- main consistent for long periods of time, punctuated occasionally by periods of rapid change, especially when selective pressures change or a new variant arises within a species with a significant advantage. First proposed by paleontologists Niles Eldredge and Stephen Jay Gould, the punctuated equilibrium model argued against the assumption that evolutionary change would always be gradual and consistent, also seeking to explain why some species often appeared to be unchanged for very long periods in the fossil record.

Ratchet effect

A ratchet is a type of wrench or lever that can only turn in one direction; a locking mechanism prevents the bolt or pin being turned from reversing and undoing its progress. Psychologist and evolutionary theorist Michael Tomasello used the term 'ratchet effect' to describe a cultural process through which technology, invention and knowledge no longer get lost with the death of a generation of individuals because the mechanisms for cultural transmission are sufficiently strong to prevent their loss. Advanced cultural learning, including lateral cultural transmission, meant that human knowledge became shared and cumulative, allowing our species to make great technological advances.

Related Terms: Cognitive niche, Lateral transmission

Recessive

A recessive gene is a gene that only affects phenotype, or the appearance of an organism, in the absence of the dominant gene. Usually, this requires that the offspring receive a recessive gene from both parents because the presence of a single dominant gene will mask the presence of the recessive variant although, because of particulate inheritance, the recessive trait might still be passed on to offspring.

Related Terms: Allele, Discreet, Dominant gene, Particulate inheritance

Recombination

The production of new, novel DNA sequences through reproduction, either sexually or asexually. During meiosis, the cell division process that produces germ cells (sperm and egg) with only half of a full complement of chromosomes, parts of the chromosomes can ‘cross over,’ exchanging genetic information. The process can lead to novel sequences and combinations of the two parents traits.

Related Terms: “Red Queen” theory, Mutation, Sex

“Red Queen” theory

Taking its name from Alice’s race with the Red Queen, in Lewis Carroll’s *Through the Looking Glass*, the Red Queen theory points out that, in evolution, species must evolve and change constantly because other species, including competitors, predators, and parasites are all evolving at the same time. The Red Queen theory explains why species that were once well adapted can still go extinct, and why sexual reproduction, including the variation produced by genetic recombination, may provide a decisive advantage for a sexually-reproducing species.

Related Terms: Recombination

Retrovirus

An RNA-based virus that builds a DNA version of itself (the reverse of the usual process, thus the name ‘retro-virus’), so that it can insert itself into the nuclear DNA of a cell. A special variant of a retrovirus is an endogenous retrovirus, a virus that successfully writes itself into the germ-line DNA, thus being there from the conception of the host.

Related Terms: Endogenous, RNA

RNA

Ribonucleic acid (RNA) is a family of large biological molecules like DNA. Unlike DNA, RNA tends to be a single-strand structure of nucleotides. RNA serves to send messages and mediate the actions of DNA, controlling gene expression, signaling within a cell, or helping to build proteins from the coding portions of DNA. Some viruses are RNA strands, rather than DNA.

Related Terms: Retrovirus

Secondary sexual characteristics

Traits that differ between males and females of a species, but are not directly linked to reproduction are called secondary sexual characteristics. For example, in humans, men and women differ on a range of traits not directly linked to reproduction, such as the distribution of fat on their bodies, the over-body musculature, and the pattern of hair growth on their bodies. In some cases, secondary sexual characteristics are the result of sexual selection.

Related Terms: Sexual selection

Sex

In species that reproduce by combining gametes to form offspring, some contribute identical gametes (isogamy). When the two types do not contribute similar gametes — they are characterised by anisogamy, or difference between sperm and egg -- the sex contributing the larger gamete or 'egg' is female, and the sex contributing the smaller gamete or 'sperm' is male. In many animals, females possess XX chromosomes, and males possess the XY chromosomes (birds, some fish and crustaceans have a different chromosomal mechanism for determining sex).

Related Terms: Anisogamy, Estrogen, Gender, Hermaphrodites, Recombination, Sex-determining region of the Y chromosome (SRY), Testosterone

Sex-determining region of the Y chromosome (SRY)

The sex-determining region of the Y chromosome, or 'SRY,' codes for a protein that initiates development of the male testes. SRY is (as its name suggests) located on the Y chromosome, so is present in most males; if the gene has a mutation or is defective, even though a person's body has the Y chromosome, male genitalia will not develop (one form of this is Swyer syndrome, in which individuals look female but are sterile). A woman with XX chromosomes (normal) can have the SRY gene, leading to de la Chapelle syndrome, a rare chromsomal disorder in which individuals appear male but are infertile, and some have other physiological feminsation. SRY is not the only gene that can determine male sex, as other mechanisms do so in some species.

Related Terms: Estrogen, Hermaphrodites, Sex, Testosterone

Sexual revolution

Usually, social scientists use the term 'sexual revolution' to refer to the period from the 1960s through 1980s, during which changes in reproductive technologies (such as birth control), human rights, social mores, and laws in many Western countries led to a rapid change in sexual behaviour, including increased divorce, sex prior to marriage, increased numbers of sexual partners, greater liberty for women, and decreased repression of homosexuality and other alternative lifestyles.

In this course, we argue that humanity has undergone a number of sexual revolutions, including a radical but slower change in the way that our ancestors reproduced to support our increasingly altricial infants, more complex and enduring social networks, and changed pat- terns of childrearing. Biological factors such as decreased sexual dimorphism and concealed estrus, as well as less evidence for direct physical competition or sperm competition among hominin ancestors — unlike gorillas and chimpanzees, for example — also point to this distinctively human type of reproductive strategy.

Related Terms: Altricial, Concealed estrus, Dimorphism, Direct competition, Sperm competition

Sexual selection

An intraspecific form of evolutionary competition in which individuals compete to out-reproduce other members of their sex. Sexual selection helps explain why members of a species may develop traits that are not necessary or advantageous for survival; they may be used, instead, to compete for mates or to reproduce more. Sexual selection takes two forms: direct competition and mate choice. One hallmark of sexual selection is that the process tends to produce dimorphism, as the selective pressures in reproduction on males and females are not the same.

Related Terms: Dimorphism, Direct competition, Intraspecific competition, Mate choice, Parental investment, Secondary sexual characteristics, Sperm competition, Trivers' hypothesis

Social cognition

Forms of intelligence, perception, memory and other cognitive abilities that are used specifically in relations with conspecifics, or members of the same species. Humans appear to have more sophisticated social cognition than other apes even at a very young age, a gap even greater than that found in our ability to anticipate cause-effect, for example, in the physical world. The greater social cognition may be a result of intense intraspecific social competition, mate choice, or inter-group competition, with benefits for those hominins who were better able to perceive each other's thoughts and intentions, strategise, and cooperate.

Related Terms: Emotionally modern, Machiavellian intelligence

Speciation

The evolutionary process that turns a population, originally of a single species, into two or more distinct species, usually through a combination of reproductive isolation (which halts gene flow) and diversifying selection or genetic polymorphisms. Often, determining precisely when speciation has occurred is difficult because populations may be geographically isolated, for example, if a population has occupied a new niche.

Related Terms: Diversifying selection

Sperm competition

A form of direct sexual competition in which, because females mate with multiple males while fertile, male sperm competes directly with other males' sperm. The result can be extremely high sperm production or defensive mechanisms like semen that acts to plug the vagina or attacks subsequent sperm. Many primatologists point to the large testes of male chimpanzees, and the fact that females copulate with many males while in estrous, as an example of sperm competition.

Related Terms: Sexual revolution, Sexual selection

Stabilising selection

Stabilising selection leads to a decrease in genetic variation over time as selective pressures produce an ideal state for a trait, making variation a selective disadvantage. Stabilising selection can produce long-term consistency in a species' trait, unlike directional or diversifying selection. Because most traits in organisms are consistent over time, stabilising selection is thought to be the most common type of selective pressure.

Related Terms: Directional selection, Diversifying selection

Symbiogenesis

The merging of two separate, symbiotic species into a single organism, first proposed by Konstantin Mereschkowsky and later advocated by Lynn Margulis. Advocates of symbiogenesis argue that slow genetic change through mutation and selection is insufficient to ex- plain evolution, especially the rise of multi-cellular organisms and complex biological structures. Symbiogenesis gained additional support from the close study of chloroplasts and mitochondria, two organelles found in complex cells, which suggests a symbiogenetic origin for eukaryotic life.

Related Terms: Chloroplasts, Endosymbiotic theory, Eukaryotic cells, Mitochondria, mtDNA, Symbiosis

Symbiosis

A close, long-term relationship between two species in which both gain benefits from the presence of the other. In some cases, symbiosis is obligatory: one species cannot survive without the other. Symbiosis can include a species living on or inside another species, or less intimate relationship.

Related Terms: Endosymbiotic theory, Microbiome, Parasite, Symbiogenesis

Teleological error

'Telos' is the Ancient Greek word for 'goal' or 'purpose.' The teleological error in evolutionary thinking is assuming that evolution itself has a goal, or that evolution has a clear direction or inevitability, which is most likely in thinking of humanity is the 'end' or 'highest' expression of evolution. As a natural process, evolution does not have a design, that is, a fore- thought or intentional plan. Thinking teleologically about evolution, including assuming that humanity is the highest expression of evolution, a form of anthropocentric thinking, is a common error.

Related Terms: Anthropocentric, Great Chain of Being, Kluge

Testosterone

Testosterone is a steroid hormone of the androgen group, found in a wide range of vertebrates. Testosterone is secreted primarily by the testes in men, and by the ovaries in women although some is also produced by the adrenal gland. Testosterone is essential in the masculinisation process through which male bodies form and mature, and testosterone levels tend to be around seven or eight times higher in men than in women, although they fluctuate in both.

Related Terms: Estrogen, Sex, Sex-determining region of the Y chromosome (SRY)

Trivers' hypothesis

Robert L. Trivers recognised that, because females typically invest more in their offspring (see parental investment), males will have to compete for a chance to reproduce, unless the parental investment of males is as high or higher than female parental investment. Trivers' hypothesis predicts which sex will be subject to sexual selection, helping evolutionary theorists to better understand intraspecific competition in humans and others species.

Related Terms: Intraspecific competition, Parental investment, Sexual selection

Vestigial organ

Vestigial organs have lost a particular function or changed function significantly over the course of an organism's evolutionary history. Although some people think of vestigial organs as 'useless,' even organs that have lost a major function often continue to serve a different purpose subsequently. In humans, for example, the appendix has lost most of its older function in the digestive system, but it continues to serve an immunological function and also can provide a reservoir of gut flora in event of a serious gastro-intestinal infection. Unlike atavisms, vestigial organs are common to all or nearly all members of a species.

Related Terms: Atavism

VISTA

Variation + Inheritance + Selection over Time leads to Adaptation

One way to remember the factors that need to be present for natural selection to occur. The VISTA acronym highlights the roles of variation and the necessity of inheritance; the absence of either (such as non-heritable variation) prevent adaptation from occurring through natural selection.

Related Terms: Fitness, Mutation

Weaning

The transition from nursing to subsisting on an adult diet and eating independently in mammals. The appropriate age to wean humans is the subject of great controversy, and norms for weaning — as well as strategies to do it — differ widely between and within many cultures. In Australia, almost half of all children are weaned by six months of age, the minimum recommended by the World Health Organisation, with some starting to wean their children al- most immediately after birth. Anthropologist Kathy Dettwyler, using comparative research with other species and growth trends in humans, suggests that a minimum age for weaning in our hominin ancestors may have been around 2.5 years, but with a maximum of 7 years of age.

Weismann barrier

The Weismann barrier is a principle argued by August Weismann that germ cells create body cells, but that what happens to bodily cells (somatic cells) cannot influence the constitution of germ cells. Put simply, nothing you do during your life except survive and reproduce influences your offspring because the germ cells in your sperm or eggs is unchanged byyour experience. The Weismann barrier was a definitive rejection of Lamarck's principle of the inheritance of acquired traits. The Weismann barrier was once thought to be unbreachable, but new findings, especially in epigenetics, suggest that some acquired traits may affect germ cells or transmit mechanisms that affect gene expression.

Related Terms: Bodily cells, Epigenetics, Inheritance of acquired traits

Wernicke's area

A region of the human brain's cortex behind the ear on the dominant side (left hemisphere in most people) that has an important role in the comprehension of spoken language. The area is name for German psychiatrist and neurologist Carl Wernicke, who first hypthesised about the region's role in speech comprehension after examining patients with brain injuries leading to aphasia, a disruption in speech abilities that does not affect other forms of intelligence. In particular, a lesion in Wernicke's area can lead to Wernicke's aphasia, an inability to understand spoken language while still being able to speak.

Related Terms: Broca's area

Xerophyte

An organism adapted to survival in extremely dry environments (deserts).

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About the author

Greg Downey is Associate Professor in Anthropology at Macquarie University in Sydney, Australia, where he teaches about human evolution, psychological and economic anthropology, and human rights. Greg did his doctoral research at the University of Chicago before teaching at the University of Notre Dame (USA). He relocated to Australia in 2005.

Greg has done research on capoeira in Brazil, with mixed martial arts fighters in the US, and with rugby players and coaches in Australia. He writes extensively on the relationship between brain and culture, especially skill acquisition, sensory training, and developmental dynamics. You can read about his work on the weblog Neuroanthropology at the Public Library of Science (PLOS). This book contains some links to his relevant online writing at the PLOS Neuroanthropology weblog.

Greg is co-editor, with Daniel Lende, of the recent book, *The Encultured Brain: An Introduction to Neuroanthropology* (MIT Press). Greg's previous books include *Learning Capoeira: Lessons in Cunning from an Afro-Brazilian Art* (Oxford University Press) and, with Melissa Fisher, *Frontiers of Capital: Ethnographic Reflections on the New Economy* (Duke University Press).

When he’s not being an anthropologist, Greg, his wife, Tonia, and their daughter, Mikhaela, breed horses on the south coast of New South Wales, helped with unceasing enthusiasm by their dogs, Louis and Roxy. Although proudly from St. Louis in the U.S., Greg’s now a ‘dinky die’ Australian, even a mad keen cricket fan.

If you enjoyed this book, please consider learning more, either about the author, Greg Downey, or about Enculture Press.

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