“Nothing in biology makes any sense except in the light of evolution.”

T. Dobzhansky
What is Evolution?

Descent with modification:

Descent via common ancestry
Modification via natural selection

Aim:

Understand the history and diversity of life.
Evolutionary Thinking as a Paradigm Shift

Thomas Kuhn proposed that major advances in science are rare true scientific revolutions involve fundamental changes in the way that we view the world.

Once such a revolution takes place, the world is never seen or understood in the same way.
Evolutionary biologists, like all scientists

Generate hypotheses.

These hypotheses **must be:**

- Testable
- Falsifiable
Our Approach: Methodological Naturalism

Methodological naturalism:

The strategy of trying to explain the world based solely on natural phenomena is fundamental to the scientific method and is at the heart of modern evolutionary biology.
Over the Next Four Weeks

Week 1 (today): Overview, natural selection in operation.

Week 2 (July 30): How to do we get new species? How do we lose species?

Week 3 (August 6): The evolution of behavior.

Week 4 (August 13): Evolution and medicine.
ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE:

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE
FOR LIFE.

By CHARLES DARWIN, M.A.,
FELLOW OF THE ROYAL, BOTANICAL, LICEAN, ETC., SOCIETIES;
AUTHOR OF "JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE
ROUND THE WORLD."

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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THE

DESCENT OF MAN,

AND

SELECTION IN RELATION TO SEX.

By CHARLES DARWIN, M.A., F.R.S., &c.

IN TWO VOLUMES.—Vol. I

WITH ILLUSTRATIONS.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1871.

[The right of Translation is reserved.]
Darwin summarized his insights on evolution in what he called "two great laws."

The First Law:

The “environment” selects upon variation in the traits of individual organisms.
Darwin’s First Law

The “environment” selects upon variation in the traits of individual organisms.

Some variants have higher rates of reproduction than others.

Those variants with higher rates of reproduction increase in frequency.

In a nutshell, that is the process of natural selection.
When Darwin wrote of the "environment" he meant the living (organic) and nonliving (inorganic) environment that set the stage on which natural selection operates.
Darwin’s First Law

Natural selection is a process that explains both

how the characteristics of organisms change over time, and

why organisms are well-suited to their environments.
Darwin’s First Law

“Natural selection works by either now adapting the varying parts of each being to its organic and inorganic conditions of life or by having adapted them during past periods of time.”
Darwin’s Second Law

Common ancestry of living things

All species have descended from one or a few common ancestors.
CHAPTER I.

VARIATION UNDER DOMESTICATION.

Artificial Selection: Pigeons

Rock Pigeon
Artificial Selection: Pigeons

Every generation, select birds with the whitest plumage.
Artificial Selection: Pigeons
Artificial Selection on Pigeon Behavior
Artificial Selection:
Pets and Livestock
Artificial Selection: The Foods We Eat

Humans have been selectively breeding grains, vegetables and the like for more than 11,000 years.
Artificial Selection: The Foods We Eat

In each generation the “best” plants—for example, the

- hardest
- quickest growing
- most productive
- best tasting
- etc…

Are chosen as the parental stock for the next generation.
Artificial Selection: The Foods We Eat

Darwin used strawberries as an example of artificial selection:

“As soon...as gardeners picked out individual [strawberry] plants with slightly larger, earlier, or better fruit, and raised seedlings from them, and again picked out the best seedlings and bred from them, then, there appeared ... those many admirable varieties of the strawberry which have been raised during the last thirty or forty years” (Darwin 1859, pp. 41–42).
In the case of natural selection, one can think of nature as the **selective agent**.

"Man can only act on external and visible characters;

Nature cares nothing for appearances, except in so far as they are useful to any being.

She can act on every internal organ, on every shade of constitutional differences, on the whole machinery of life"
“It may be said that natural selection is daily and hourly scrutinising, throughout the world,
“It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest;
Darwin’s Insights: Phrase by Phrase

“It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good;
Darwin’s Insights: Phrase by Phrase

“It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life.
“It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages...
Natural Selection

Natural selection is the inevitable consequence of three simple conditions:

1. Variation in the trait under study
2. Differential reproductive success (fitness differences)
3. Inheritance

The process of natural selection produces adaptations.
A trait is an adaptation if it:

has been shaped by natural selection to serve the same primary function or functions that make it beneficial today.
Case Studies of Natural Selection
Natural Selection
Coat Color in Oldfield Mice

*Peromyscus polionotus*
Natural Selection
Coat Color in Oldfield Mice

A set of eloquent studies by Hopi Hoekstra and her colleagues has examined the process of natural selection for coat color in populations of the oldfield mouse, *Peromyscus polionotus*.
Throughout most of its range, *P. polionotus* is uniformly dark in coloration.

But on Santa Rosa Island off the gulf coast of Northern Florida and along the nearby beaches and barrier islands mice often display a much lighter coat color.
Natural Selection: Variation

- Northern Florida

- Anastasia Island beach mouse (N=20)
- Pallid beach mouse (extinct) (N=8)
- Southeastern beach mouse (N=20)

- Alabama beach mouse (N=20)
- Perdido Key beach mouse (N=20)
- Santa Rosa Island beach mouse (N=40)
- Choctawhatchee beach mouse (N=20)
- St. Andrew's beach mouse (N=20)
- Oldfield mouse (N=40)
A series of genetic studies have identified several genes that are responsible for much of the coat color variation in *P. polionotus*. The first of these genes is the *Mc1r* gene, which influences mammalian coat color and avian plumage color in many species.
Mc1R control the type of pigment that is created and incorporated into hair (or feathers).

\[ \text{\(\bullet\) = } \alpha \text{ MSH hormone} \]

Eumelanin production leads to dark fur.
Natural Selection: Inheritance

Production of **eumelanin** produces dark fur
Hoekstra and her colleagues have documented two different mutations in the beach populations of *P. polionotus* where oldfield mice have light coat color.
Receptor is broken

\(\alpha\) MSH hormone can’t bind to it.

Light color is produced
A different mutation produces lots of another chemical (ASP) that binds to receptor.

When that chemical binds, you get light color, not dark color.
Natural Selection

Fitness Differences

The *fitness* of a trait or gene is defined as the expected reproductive success of an individual with that trait or gene, *relative* to other members of the population.
Natural Selection
Fitness Differences

A
53.7% Captured
32.8%

B
32.1% Captured
55.1%

C
12.2% Captured
23%
Natural Selection

Fitness differences
Natural Selection

Fitness differences
Natural Selection: Interpopulational Differences in the Guppy
Interpopulational differences in the Guppy

Low-predation site
Females produce fewer, but bigger offspring

High-predation site
Females produce many small offspring

Predator (Rivulus hartii)
Prey (Guppies)

Predator (Grenicichla alta)
Prey (Guppies)
<table>
<thead>
<tr>
<th></th>
<th>High Predation</th>
<th>Low Predation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Color</strong></td>
<td>Dull</td>
<td>Bright</td>
</tr>
<tr>
<td><strong>Schooling Behavior</strong></td>
<td>Large, tight school</td>
<td>Weak, loose schools</td>
</tr>
<tr>
<td><strong>Antipredator Behavior</strong></td>
<td>Very alert</td>
<td>Less alert</td>
</tr>
<tr>
<td><strong>Number and size of offspring</strong></td>
<td>Many, small</td>
<td>Fewer, large</td>
</tr>
</tbody>
</table>
Experimentally manipulate selection pressures to test hypothesis.
## Results of Selection Experiments

<table>
<thead>
<tr>
<th></th>
<th>Descendants of high predation fish living in low predation area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Color</strong></td>
<td>Dull to Bright</td>
</tr>
<tr>
<td><strong>Schooling Behavior</strong></td>
<td>Large, tight school to Weak, loose schools</td>
</tr>
<tr>
<td><strong>Antipredator Behavior</strong></td>
<td>Very alert to Less alert</td>
</tr>
<tr>
<td><strong>Offspring # and size</strong></td>
<td>Many small to fewer, large</td>
</tr>
</tbody>
</table>
Imagine that you were an evolutionary biologist with superhuman powers that you could use in the service of your research. Suppose that you could:

- Watch as tens of thousands of generations of evolution take place before your eyes.
- Manipulate many aspects of the abiotic environment
  - nutrient availability
  - temperature
  - spatial structure
- Manipulate many aspects of the biotic environment
  - adding or removing
  - competitors
  - predators
  - parasites
Natural Selection
A Thought Experiment

- Create multiple parallel universes with the same starting conditions in which to watch evolution unfold in duplicate, triplicate and so on.

- Move organisms around in a time machine so that they could meet—and compete against—their ancestors or their descendants.

- Go back in time to re-run evolution from any point, under the same or different environmental conditions.

- Easily measure both allele frequencies, and the relative fitness of organisms down to a tenth of a percent.
Natural Selection

One of the most striking examples is work by Richard Lenski and his colleagues who have been tracking evolutionary change in *Escherichia coli* for well over 70,000 generations.
February 24, 1988

*E. coli* colonists were placed in twelve parallel “universes”

Differed only by an unselected “marker gene” that lets researchers keep track of which experimental line is which.
Every day for the last 36 years, researchers transfer cells from each of the 12 lines into fresh growth medium.
Periodically a sample of the cells from each line is frozen in a -80 degree C freezer.
Natural Selection
70,000 generations in *E. coli*

**Step 1.** To initiate experiment, take a single bacterial clone and create 12 genetically identical lines.

**Step 2.** Carry out daily protocol for 13,000+ days.

**Step 3.** Evolved strains and frozen ancestors are now available for wide range of evolutionary studies.

- Each day:
  - Grow
  - Store samples in ~80°C freezer

- 1.
- 2.
- 3.
- ...
- 12.
What can you do with an experimental system like this?
Natural Selection
70,000 generations in *E. coli*

Would the same traits that evolve in Universe 1, Universe 2, Universe 3...?

Or would you see something completely different in each Universe?
Lenski and his colleague Michael Travisano set out to address this question by:

Comparing what happened in the twelve parallel runs of evolutionary history in their experiment.
The volume of cells significantly increased over the first two to three thousand generations.
Natural Selection
70,000 generations in *E. coli*

Removed a sample of *E. coli* cells after every 500 generations and then deep-froze them.

These cells could be thawed at any time and allowed to compete against their descendants in order to see whether the descendants had increased in fitness.
Was this a quirk of chance or an evolutionary near-necessity?
Natural Selection
70,000 generations in *E. coli*

Cell size increased in all 12 universes
Natural Selection
70,000 generations in E. coli

Fitness increased in all 12 universes
With the drastic environmental changes associated with human-caused climate change, human population growth, large-scale production of toxins, and more, many scientists argue we are now living in the **Anthropocene Era**.
Anthropogenically driven climate change, largely the result of increased emission of CO$_2$ has led to dramatic changes in annual temperatures all over the planet.

Spring thaws in many places in the United States have been arriving earlier and earlier.
Evolution in The Anthropocene Era: Hatch Date

Reproduction and survival in tree swallows (*Tachycineta bicolor*).
By breeding earlier in the season, birds risk being exposed to cold snaps that have significant effects on hatchling survival.
Tree swallow nestlings hatched between 2011-2015 were twice as likely to experience a cold snap during their early development as birds hatched in the 1970s, leading to an increase in the number of nests in which no chicks survived.
Evolution in The Anthropocene Era: Hatch Date

A mismatch now exists between adaptations that were crafted by natural selection for optimal breeding dates and Anthropogenic-driven changes in temperature.
How Can Natural Selection Generate Complex Structures with Multiple Intricate Parts?
Natural Selection and Complexity

Darwin generally portrayed natural selection as a slow process acting on very small differences between individuals.

It is easy to see how this process could lead to gradual changes in

Fur coloration

Cell size

Hatch date

...
Natural Selection and Complexity

But how might natural selection operate as a genuinely creative process?

How might it generate complex structures?
If natural selection operates by gradual increments, then:

the eye must be preceded by one half of an eye or a quarter of an eye

and what good is that?
Natural Selection and Complexity

We will examine two possible explanations for the evolution of such complex traits.

1. Adaptationist explanation
2. Exaptationist explanation
Natural Selection and Complexity

We will examine two possible explanations for the evolution of such complex traits.

1. Adaptationist explanation

Each intermediate step on the way toward the evolution of complex traits was favored by natural selection and served a function similar to the modern-day function.

Example: eye
Natural Selection and Complexity

How could such a complex trait ever evolve in the first place?

Darwin raised this very issue in *The Origin of Species*:

“To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances for admitting different amounts of light... could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree.”
But Darwin hypothesized natural selection could and did surmount this difficulty via small successive changes each of which provided a benefit compared to the last version of the eye.
"Yet reason tells me if…

the eye does vary ever so slightly, and the variations be inherited, which is certainly the case;

and if any variation or modification in the organ be ever useful to an animal under changing conditions of life,

then the difficulty of believing that a perfect and complex eye could be formed by natural selection,

though insuperable by our imagination,

can hardly be considered real."
Dan-Erik Nilsson has reconstructed just such a sequence by which the eye might have evolved.
Nilsson begins with a creature that has a very simple light-sensitive eyespot:

can distinguish between light and dark.
Nilsson next uses computer simulations to demonstrate what happens when the eyespot became slightly depressed.

The cells on the surface of the eyespot are pushed in on themselves, creating a cup-like structure.

Produces a new visual system able to detect shades of light.
Natural Selection and Complexity
Adaptation and The Case of the Eye

If a simple aperture, which focuses incoming light by constricting the opening through which light enters, is added to the system we have an eye that acts like a pinhole camera creating a sharper image.
If a refractive lens is added, we have an even more complex eye, capable of detecting sharper images and better at detecting motion.
Natural selection and Complexity
Adaptation and The Case of the Eye

If a gel-like substance (the vitreous body) is added behind the lens it sharpens the image.

This sort of eye can be found in creatures such as octopuses and humans.
Exaptationist explanation:

intermediate stages of complex traits were functional and selected but did not serve the same function in the past as they do today.

Examples:

- cranial sutures
- feathers
In mammals, cranial sutures are the fibrous connective tissue joining the bones that make up the skull.
In *The Origin of Species*, Darwin wrote

“The sutures in the skulls of young mammals have been advanced as a beautiful adaptation for aiding parturition, and no doubt they facilitate or may be indispensable for this act.”
Darwin argued that easing movement through the birth canal was *not* the original function of sutures.

Sutures do that now
but that could not have been their original function.

Why?

“sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg.”
Cranial sutures could not have evolved to aid the birth process in mammals as they were present before the evolution of mammalian reproduction.
The original function of cranial sutures was probably to allow the rigid protective cranium to expand with a growing brain.
Feathers play such a prominent role in bird flight it is tempting to think that feathers have always been selected in relation to their effect on flight, but

The origin of feathers predated in the origin of flight

Time
Natural Selection and Complexity
Exaptation and the Case of Feathers

What might have been the original function(s) of feathers?

Two possible ancestral functions: 1) thermoregulation, and 2) prey capture.
Natural Selection and Complexity
Exaptation and the Case of Feathers

Feathers may have served a thermoregulatory function controlling heat loss and gain in early birds.

This may have been especially important because:

early birds had especially high metabolic rates may have been susceptible to thermoregulation problems.
Contour feathers are already seen in Archaeopteryx, an early bird-like dinosaurs help control thermoregulation
Natural Selection and Complexity
Exaptation and the Case of Feathers

Thermoregulation is the most widely accepted early function for feathers, but it is not the only possibility.

Evidence from the head and jaw of Archaeopteryx:

Suggests that it fed on large insects

feathers may have served as a large “snare” or net that the animal used to capture large insects.