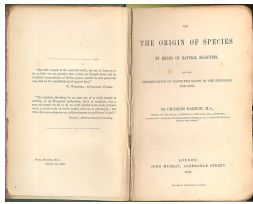


Darwin's *On the Origin of Species*



William Paley (1743-1805)



- "In order to pass the B.A. examination, it was, also, necessary to get up Paley's Evidences of Christianity, and his Moral Philosophy. . . The logic of this book and as I may add of his Natural Theology gave me as much delight as did Euclid. The careful study of these works, without attempting to learn any part by rote, was the only part of the Academical Course which, as I then felt and as I still believe, was of the least use to me in the education of my mind. I did not at that time trouble myself about Paley's premises; and taking these on trust I was charmed and convinced of the long line of argumentation." Charles Darwin. Autobiography

2

Watchmaker Argument

- "when we come to inspect the watch, we perceive. . . that its several parts are framed and put together for a purpose, e.g. that they are so formed and adjusted as to produce motion, and that motion so regulated as to point out the hour of the day; that if the different parts had been differently shaped from what they are, or placed after any other manner or in any other order than that in which they are placed, either no motion at all would have been carried on in the machine, or none which would have answered the use that is now served by it. . . the inference we think is inevitable, that the watch must have had a maker -- that there must have existed, at some time and at some place or other, an artificer or artificers who formed it for the purpose which we find it actually to answer, who comprehended its construction and designed its use.
- "Every observation which was made in our first chapter concerning the watch may be repeated with strict propriety concerning the eye, concerning animals, concerning plants, concerning, indeed, all the organized parts of the works of nature."

3

The Lessons from the Beagle

- On the Beagle Darwin's primary task was to investigate the geology of the locations visited, but he also recorded extensively and collected samples of plant and animal life as well as fossils
 - His extensive collections were regularly sent back to England where they were displayed for scientists, establishing Darwin's reputation as a naturalist
 - They also provided the basis for ongoing analysis over many subsequent years
- Darwin kept detailed journals which also included his developing hypotheses both about geology and the distribution of life forms
 - Discovering sea fossils high in the Andes (as well as experiencing severe earthquakes in Valdivia), he speculated about the rising and sinking of continents



4

Galapagos: Finches

- On the way from South American to New Zealand, the Beagle stopped at the Galapagos Islands, recently formed volcanic islands where Darwin became impressed with the various life forms (especially birds, tortoises, iguanas).
- Of particular interest with the finches (mockingbirds)
 - All the island species were similar to the one species found on the mainland
- He observed major specializations in beak shape and size:
 - Large, medium and small seed and insect-eaters, cactus eaters, tree-dwelling and ground-dwelling finches
- Pattern true not just of finches: similar patterns giant tortoises, lizards, etc.
- In each case, organisms exhibit traits that are useful in their local environments
 - Major question: How did they become adapted?

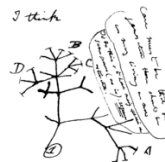


1. *Geospiza magnirostris* 2. *Geospiza fortis*
3. *Geospiza parvula* 4. *Certhidea olivacea*
Finches from Galapagos Archipelago

5

Transmutation Notebooks

- The Beagle returned to Britain in October 1836
- In early 1837 Darwin began his Notebook on the transmutation of species
- Several components of his view of transmutation (evolution) were already in place
 - Descent with modification
 - Notion of divergence from a common ancestor
 - Variation within domestic varieties
 - Variation within natural species
 - Patterns of geographic distribution (including species with traits appropriate for their environments)



I think
The letters A, B, C, D
are of value. C & B. It
first produced, B & D
with greater distinction
The former could be
formed. - heavy letter

6

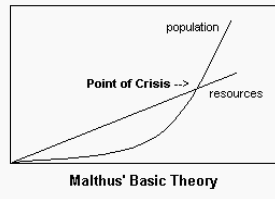
In search of a mechanism

- What is Darwin lacking at the time of the Transmutation Notebooks?
 - He has no account of heritability and how variation can arise and be passed on
 - He has no understanding of how these variants come to be adapted to their environment—no answer to Paley
- September 1838: *for amusement* Darwin read the *Essay on Population* (1798) by Rev. Thomas Robert Malthus (1766-1834)
 - Malthus, along with Adam Smith and others interested in political economy, sought to discover the *laws of society*



Malthus' laws of population

- Law 1: Food Supply grows *arithmetically*: 2, 4, 6, 8, 10, 12 . . .
- Law 2: Population tends to grow *geometrically*: 2, 4, 8, 16, 32, 64, 128 . . .
- 1st consequence: Populations always tend to outrun food supplies
- 2nd consequence: More offspring born than can survive
- 3rd consequent: There will always be competition for food (and other) resources



From competition to selection

- Overproduction means only some will survive
- That doesn't yet imply selection as survival might only depend on luck, chance, etc.
 - Must add that survival depends upon the organism's abilities to deal with the demands of competition
 - Also, that there is variability among the competitors
 - And that this variability is heritable—offspring will possess those very traits that improved the parents' ability to deal with environment demands
- Evolution by natural selection requires *heritable variation in fitness*

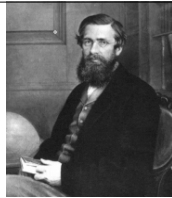
Developing the idea—Darwin's notes on natural selection

- 15-page "Essay" of 1842
- 100+ page "Essay" of 1844
- Circulated among some associates (Lyell, Joseph Dalton, Hooker)
 - They urged him to publish, but Darwin was cautious
- Chambers' *Vestiges* was published in 1844
- Darwin then detoured to work on systematics of barnacles (*Cirripedia*)—a detailed two volume work that established Darwin's reputation in biology



Goaded into publication

- Darwin received a letter in 1857 from Alfred Russel Wallace, a young naturalist living in Malaysia
- Wallace had also read Malthus and written a paper on "natural selection"
- Lyell and Hooker arranged for papers of both Darwin and Wallace to be read before the Linnaean Society in July 1858 and published in Society's *Proceedings* in August
- There was no significant response to these papers
- Darwin began feverishly writing his "Abstract," which he sent to his publisher, John Murray in June, 1859
- Published on November 1, 1859 and the first run of 1250 copies sold out that day



Structure of the *Origin*—an abstract!

1. Variation Under Domestication
2. Variation Under Nature
3. Struggle for Existence
4. Natural Selection
5. Laws of Variation
6. Difficulties on Theory
7. Instinct
8. Hybridism
9. On the Imperfection of the Geological Record
10. On The Geological Succession of Organic Beings
11. Geographical Distribution
12. Geographical Distribution continued
13. Mutual Affinities of Organic Beings: Morphology: Embryology: Rudimentary Organs
14. Recapitulation and Conclusion

Artificial Selection

- The first chapter both makes the case for variability AND tries to explain the origin of the forms found today
 - “nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds”
 - Often the differences are so minor as to be undetected except by the skilled breeder
 - “the accumulative action of Selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant power” in producing change in domestic species



Discussion Question

Why does Darwin begin by focusing on domesticated plants and animals?

He simply finds it interesting that breeders have been so successful in creating different varieties

He intends the results of his analysis of domesticated plants and animals to provide an analogy for processes at work in nature

By showing what breeders can accomplish by selecting organisms to breed he is making it plausible that processes operative today can explain the diversity of life

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The Explanatory Challenges

- The challenge of adaptation: “How have all those exquisite adaptations of one part of the organisation to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected?”



- “Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow inevitably from the struggle for life.”

Clicker Question

What is the primary factor that makes the struggle for existence inevitable for Darwin?

The number of organisms in any species tends to increase at a geometric ratio and resources don't

Organisms prey on one another and develop ways to protect themselves, creating an arms race

Storms and draught generate inhospitable conditions against which organisms must struggle

Failure of parents to keep their number of offspring at a reasonable number

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Generality of struggle

- "I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny."
- Malthus' principle: "A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product."

Clicker Question

How does Darwin characterize Natural Selection?

Preservation of favorable variations and the rejection of injurious variations

A process of picking out among new variants those most likely to foster reproductive success

A process like artificial selection, but only weaker and so requiring much more time

A natural force like gravity that picks out some organisms for permanent preservation

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Natural Selection

- Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? **If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind?** On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call **Natural Selection**. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic.

The power of natural selection

- “Man can act only on external and visible characters: nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life.”
- “Man selects only for his own good; Nature only for that of the being which she tends.”
- “Why, if man can by patience select variations most useful to himself, should nature fail in selecting variations useful, under changing conditions of life, to her living products? What limit can be put to this power, acting during long ages and rigidly scrutinising the whole constitution, structure, and habits of each creature, — favouring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life. The theory of natural selection, even if we looked no further than this, seems to me to be in itself probable.”

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Clicker Question

What does Darwin mean by sexual selection?

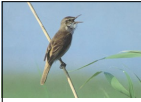
The selection of sexual species since they produce more variation and so evolve faster

The competition between males in developing traits that are attractive to females

The bitter competition, often leading to death, between members of the different sexes

The bitter competition, often leading to death, between members of one sex for access to the other

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Sexual selection



- “when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection”
- “This depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection. Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex. A hornless stag or spurless cock would have a poor chance of leaving offspring.”

Discussion Question

Why, when he writes a section on illustrations of natural selection does Darwin only offer imaginary illustrations

It would take too much time to really describe real examples

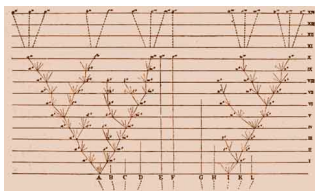
There really was no direct evidence for the actual operations of Natural Selection

It is very difficult to identify the full range of factors that affect which organisms are able to reproduce

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Creating separate species

- “As each species tends by its geometrical ratio of reproduction to increase inordinately in number; and as the modified descendants of each species will be enabled to increase by so much the more as they become more diversified in habits and structure, so as to be enabled to seize on many and widely different places in the economy of nature, *there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species.* Hence during a long-continued course of modification, the slight differences, characteristic of varieties of the same species, tend to be augmented into the greater differences characteristic of species of the same genus. New and improved varieties will inevitably supplant and exterminate the older, less improved and intermediate varieties; and thus species are rendered to a large extent defined and distinct objects.”



Repudiating Essentialism: Species

- “From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.” [*Origin*, p. 52]
- “. . . I believe species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links . . . [*Origin*, p 177]
- “Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known . . . to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. . . [W]e shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.” [*Origin*, p 485]

One origin for all species

“Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. We see this even in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree. 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.”

Natural selection not optimizing

- “Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence. And we see that this is the degree of perfection attained under nature. The endemic productions of New Zealand, for instance, are perfect one compared with another; but they are now rapidly yielding before the advancing legions of plants and animals introduced from Europe. Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature. . . . Can we consider the sting of the wasp or of the bee as perfect, which, when used against many attacking animals, cannot be withdrawn, owing to the backward serratures, and so inevitably causes the death of the insect by tearing out its viscera?”

Not optimizing



Natural selection does not grant organisms what they "need".

Not optimizing - 2

- "As natural selection acts by competition, it adapts the inhabitants of each country only in relation to the degree of perfection of their associates; so that we need feel no surprise at the inhabitants of any one country, although on the ordinary view supposed to have been specially created and adapted for that country, being beaten and supplanted by the naturalised productions from another land. Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect; and if some of them be abhorrent to our ideas of fitness. We need not marvel at the sting of the bee causing the bee's own death; at drones being produced in such vast numbers for one single act, and being then slaughtered by their sterile sisters; at the astonishing waste of pollen by our fir-trees; at the instinctive hatred of the queen bee for her own fertile daughters; at ichneumonidae feeding within the live bodies of caterpillars; and at other such cases. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed."

Grandeur of evolution

- "Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely the production of the higher animals, directly follows. There is a grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling 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." (last paragraph of *Origin*)