The Extended Phenotype
The Long Reach of the Gene.
1999
Richard Dawkins

1. Necker Cubes and Buffaloes

This is a work of unabashed advocacy for a way of looking at familiar facts and ideas, not a new theory. Advocacy would be inappropriate for a new scientific theory.

One of the aims of the book is to switch emphasis from the individual body as a focal unit of functional discussion. A smaller unit, the active germ-line replicator, is more appropriate.

“it is a poor advocate that leaps precipitately to his conclusion when the jury is sceptical.” pg.8

2. Genetic Determinism and Gene Selectionism.

The belief that genes are somehow super-deterministic, in comparison with environmental causes , is a myth of extraordinary tenacity...” pg.11

“to a working biologist, causation is a rather simple statistical concept.” pg 11 One cannot demonstrate causation, only statistical likelihood.

“.. all genetic causes have to work in the context of an environment of some kind” pg 12

“Undoubtedly, genetic variance is a significant cause of much Phenotypic variance in observed populations, but its effects may be overridden, modified, enhanced, or reversed by other causes. Genes may modify the effects of other genes, and may modify the effects of the environment. Environmental events, both internal and external, may modify the effects of genes, and may modify the effects of other environmental events.” pg 13

“I think a confusion between evolution and development, is then, partly responsible for the myth of genetic determinism.” pg14 Another cause of the myth is the idea that genes are programmed like the inflexible code of a computer.

“Gene selectionism, which is a way of talking about evolution, is mistaken for genetic determinism, which is a point of view about development.” pg. 18

Darwinian adaptation is that adaptation produced by natural selection.

“In order for a trait to evolve by natural selection it is necessary that there be genetic variation in the population for such a trait.” Lewontin 1979b pg 20

If there is strong selection in favour of some trait then the variation may all be “used up”

A gene is not a cistron for the production of a particular protein, it is a tendency. A gene need not have a single-locus – but it is convenient to speak as if it did when the discussion is about some other aspect of the genetic variation. It is not necessary to know how the gene acts (however complex) only that it results in a statistical variation. Also, a mutation at a single-locus may disrupt a particular phenotype but this does not mean the original natural selection involved that locus, it may have been constant throughout (for instance blindness disrupts reading)

It is always legitimate to postulate genes for any discussion or Darwinian adaptation” pg 27.

3. Constraints on Perfection.

“Adaptionism is defined as – that approach to evolutionary studies that assumes without further proof that all aspects of the morphology, physiology and behaviour of organisms are adaptive optimal solutions to problems.” pg 30. Dawkins lists six reasons why adaptionists should be cautious and another three which have been proposed but are unconvincing.

Three unconvincing reasons. The debate over neutral mutations is about phenotypic effect and is irrelevant to a discussion on adaptation. Allometry is where a deer's antlers grow out of proportion to the body mass and this is not necessarily an example of adaptation but rather a phenotypic by-product of some other adaptation. Similarly with pleiotropy where the presence of one gene has more than one phenotypic effect.

Time Lags. Most adaptations were to environmental pressures of long ago and man has increased the rate of environmental change drastically. Example: moths navigate by maintaining a constant angle to starlight which causes them to fly into candles in a spiral. Example: human homosexuality – no genetic effect is context free – it is dependent on the environment.

Historical Constraints. Every intermediate step of evolution must work and be better than the last. “a patchwork of make-shifts pieced together, as it were, from what was available when opportunity knocked, and accepted in the hindsight, not the foresight, of natural selection” Pittendrigh 1958 pg 39.

Available Genetic Variation. There can be no evolution without genetic variation and the rate of evolution is proportional to the amount of variation. Constraints are introduced when a species begins to evolve in a particular direction. Satisficing is evolving just enough to stay alive, meliorizing (from better) allows for competition and Optimising is an engineering (optimum).

Constraints of costs and materials. Every adaptation has a cost or at least a series of tradeoff's. Reverse optimality searches for a set of constraints for which the observed behaviour is optimum.

Imperfections at one level due to selection at another level. “The kind of adaptations we would see if selection acted at the level of the group would be quite different from the adaptations that we would expect if selection acts at the level of the individual” pg 50 “ The gene is often the most appropriate level.

Mistakes due to environmental unpredictability or malevolence. Evolution adapt to some type of average environmental conditions but the specific conditions may be quite difference. Other competitive trickery is even more unpredictable.

4. Arms Race and Manipulation.

Some animals cause other animals to perform actions which are against their best interests and this is not necessarily just a time-lag effect but can be sustainable in geological time. These manipulations also happen within a family.

The manipulations will result in a arms race of adaptation and counter-adaptation. Examples, insect sexual dirty tricks, cuckoo chicks

Darwin considers all animal communication as manipulation of signal-receiver by signal-sender.

Inanimate objects can only be moved by brute force but other animals can be manipulated by more subtle and efficient means.

“What entitles us to assert that the female is 'in control of her own muscles and limbs'?” pg 60 Example: cricket songs, baby crying.

The Looser in the manipulation does not necessarily go extinct. The 'rare-enemy effect' is an example of asymmetry in selection pressures where the 'winner' is a rare species that represents negligible risk to the 'loser' – it is simply not worth making a counter-adaptation. The 'dinner/life principle' is where the rabbit runs faster than the fox because it's life is at stake while the fox is only running for his dinner. Examples, angler fish, cuckoo,

The manipulations may not be so different to drug addiction in humans where a drug controls the nervous system of the addict. Examples birds preened by other birds or ants, cuckoo chicks in a host nest, ant queens murdering another queen and assuming the throne, slave-making ants, Mothers prefer children to help rear siblings while children are indifferent to rearing siblings or their own children.

Animals are quite likely to work hard and vigorously for the good of some other individual's genes, and to the detriment of their own.

5. The Active Germ-line Replicator.

In 1957 Benzer split the single unitary gene concept in to three: the muton is the minimal unit of mutational change; the recon is the minimum unit of recombination; a cistron is effectively equivalent to the unit responsible for synthesising one polypeptide chain. Dawkins suggests a fourth unit, the optimon that is the unit of natural selection.

Adaptation, for the good of ..... what? The active germ-line replicator, not the species or the individual or .... the nucleotide. The active germ-line replicator is the optimon.

A successful replicator has Longevity, Fecundity and Fidelity.

The fidelity may not be perfect but the important point is that copy errors are cumulative in a chain of replicators.

Any portion of the chromosome is a potential replicator. Natural selection is the differential survival of replicators relative to their alleles. A replicator can be said to have a half life measured in generations. The replicator concept allows for within cistron cross-over.

“An active replicator is a chunk of genome that, when compared to its alleles, exerts phenotypic power over the world, such that its frequency increases or decreases relative to that of its alleles.” pg 91.

A single nuceotide is not a replicator nor is the whole sexual genome.

The study of a gene for any phenotypic character always refers to the difference between two alleles.

6. Organisms, Groups and Memes: Replicators or vehicles?

An organism is not a replicator because a change in the organism is not passed on to the next generation. A group even less. *There is an extended discussion and defence of Darwin's ideas in response to critics.*

“A meme should be regarded as a unit of information residing in a brain.” pg 109. It is distinct from its phenotypic effects. A meme may or may not have any relevance to genetic replication.

“An important aspect of the environment which selects between alleles at any one locus is the genes that already dominate the gene-pool at other loci.” pg 111. Similarly for memes. There are also many differences between genes and memes which may render the analogy redundant.

An organism is a communal vehicle for replicators. “There is a hierarchy of entities embedded in larger entities, and in theory the concept or vehicle might be applied to any level of the hierarchy.” pg 112.

“The reason that I may sound reductionistic is that I insist on an atomistic view of units of selection, in the sense of the units that actually survive or fail to survive, while being whole-heartedly interactionist when it comes to the development of the phenotypic *means* by which they survive.” pg 113

“In this book I am using the word 'vehicle' for an integrated and coherent 'instrument of replicator preservation'. A vehicle is any unit, discrete enough to be worth naming, which houses a collection of replicators and which works as a unit for the preservation and propagation of those replicators.” pg 114

7. Selfish Wasp or Selfish Strategy?

In practice it is often more useful to compare the success of alternate strategies rather than of particular organisms.

Field research into wasps revealed a strategy of digging a new burrow vs fighting for a burrow that was common to the wasp species rather than to a particular organism.

This species behavioural strategy is specific to the gene rather than to the organism which lends eight to the gene being the unit of survival rather than the organism.

8. Outlaws and Modifiers

“An 'allelic outlaw' is defined as a replicator that has a positive selection coefficient at its own locus but for which, at most other loci, there is a selection in favour of reducing its effect at its own locus.” pg 133 For example a segregation disorder is favoured at its own locus by getting itself into more than 50% of the gamete's produced.

“the beneficial effect of a gene tend to become dominant through the selection of modifiers, while its deleterious effects tend to become recessive.” pg 137

An arms race will develop between outlaws and modifiers but the outlaws will be outnumbered.

“If a segregation disorder occurs on a sex-chromosome ..... it also, ... threatens the whole population with extinction”. Pg 139 This is useful in pest control.

Selfish sperm. “With some exceptions, all the diploid cells of an organism are genetically identical, but the haploid gametes it produces are all different .... and there is therefore potential for conflict among them.” pg 141

The 'green-beard' effect is where the 'genes' appear to recognise copies of themselves in other individuals and provide favour on that basis. It can only happen where one mutation results in both the label (green beard) and the tendency to behave altruistically towards that label.

Assortive mating is the tendency of individuals to prefer to mate with individuals that genetically resemble them. This assumes self-inspection – the 'arm-pit' effect.

The green-beard effect refers to a gene specifically favouring itself not just a similar bag of genes as in the 'arm-pit' effect. 'green beard' genes are not necessarily outlaws.

The 'green beard' effect may be implausible but it is instructive.

Chimps and gorillas have a lot of similarity in their genes but there is no selection pressure between the same genes in the two species because the competition is between alleles for a particular loci and there is no possibility of a chimp/gorilla cross.

9. Selfish DNA, Jumping Genes, and a Lamarkian Scare.

“The total amount of DNA in different organisms is very variable and the variation does not make obvious sense in terms of phylogeny. .... A large percentage of the DNA in eukaryote genomes is never translated.” pg 157

“Replicability and 'spliceability' seem to be among the most salient features of DNA in its natural environment of cellular machinery” Richmond 1979 pg 158

“.... cells are home to a motley riff-raff of DNA and RNA fragments, cashing in on the perfect environment provided by the cellular apparatus. ... ...plasmids, episomes, insertion sequences, plasmons, virions, transposons, replicons, viruses. ... It is not a static structure, but a fluid community.” pg 159

“Selfish DNA is selected for its power to spread 'laterally', to get itself duplicated into new loci elsewhere in the genome.” pg 161 It is a laterally spreading outlaw' : like viruses or cancer cells.

Selfish DNA will probably have “... qualities that make for ease of duplication and insertion, and qualities that make it difficult for defence mechanisms of the cell to seek them out and destroy them.” pg 162

Selfish DNA is an outlaw in the sense that it wastes resources for duplication etc. An arms race will progress but a cruder defence against selfish DNA is that any mutation which removed a random piece of the selfish DNA would be better off.

10. An Agony in Five Fits.

The term “survival of the fittest” is misleading and used in a number of different ways:

- 'original fitness' did not have a precise technical definition and roughly meant the capacity to reproduce and survive.
- For population geneticists, fitness is an operational measure defined in terms of a measurement procedure involving not the whole organism but the genotype usually at a single locus.
- Ethologists and ecologists consider whole organisms and define 'classical fitness' as the product of survival and fecundity.
- 'inclusive fitness' (Hamilton) focusses on reproductive success - how many descendants are created.
- 'personal fitness' (Orlove) considers the effects that an individuals relatives have on its fitness.

“Individual-level thinking is superficially attractive because individuals, unlike genes, have nervous systems and limbs which render them capable of working in obvious ways to maximise ..... inclusive fitness ..... [but] individuals do do not consciously strive to maximise anything; they behave as if maximising something. ... [and neither do genes]. “ pg 188.

11. The Genetic Evolution of Animal Artefacts.

Genes have phenotypic, and behavioural effects as a result of long and complicated causal chains – so why stop at the boundary of the organism when considering the effects of genes? Examples caddis flies houses, spiders webs and beavers dams.

Termite mounds are filled with genes in termite clones – how is this so different to a eukaryote where the same genes are found in each cell? “Presumably an individual termite working in a little corner of a big mound is in a similar position to a cell in a developing embryo, or a single soldier tirelessly obeying orders whose purpose is in the larger scheme of things he does not understand. Nowhere in a single termites nervous system is there anything remotely equivalent to a complete image of what the finished mound will look like.” pg 204.

The analysis of artefacts only sensibly includes those effects that have a differential impact on the survival of the replicating entities, i.e. the footprint in the mud (probably) has no effect!

12. Host Phenotypes of Parasite Genes.

“phenotypes that extend outside of the body do not have to be inanimate artefacts; they can themselves be build of living tissue. ..... where-ever there are 'shared' genetic influences on an extended phenotype, the shared influences may be in conflict with each other rather than cooperative.” pg 210

Example: snails with trematode parasites have thicker shells because the parasite is interested in the individual snail surviving longer while the snail is attempting to strike the right balance for reproductive success.

“Flukes of the genus Leucochloridium invade the horns of snails where they can be seen through the skin, conspicuously pulsating. His tends to make birds, how are the next host in the lifecycle of the Fluke, bite off the tentacles mistaking them, Wickler (1968) suggests, for insects.” pg 212. The flukes

also tend to make the snails more light seeking.

Many examples snails, ants, bees, castration, mice, shrimps, crown galls on plants, rabid dogs.

"... the real reason why snail genes stand to gain from the same events as each other, while fluke genes stand to gain from a different set of events, is simply this: all snail genes share the same route to the next generation - snail gametes. .... If the parasite's means of genetic exit from the host's body is the same as the host's, namely the hosts gametes or spores, there will be relatively little conflict between the 'interests' of parasite and host genes. ... Mitochondria, chloroplasts, and other cell organelles with their own replicating DNA might also be good candidates for study in this connection." pg 222

Classification of parasitic and symbiotic relationships should be done on three dimensions. Firstly, the degree of difference or similarity in the methods of egress from hosts, and propagation of host genes and parasite genes. Secondly, the time of action of a parasite genes during host development where early action can have a far more powerful phenotypic effect. Thirdly the continuum from close intimacy to action at a distance.

13. Action at a Distance.

The point of interest in the chain of phenotypic effects caused by a gene is an arbitrary choice. It may be at any point within the cell, within the organism, beyond the organism or within another organism.

"An animal's behaviour tends to maximise the survival of the genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it." pg 233

"Components within a population are favoured by selection if they happen to interact harmoniously with the other components that happen to be frequent in the population." pg 240

"There are two general ways in which harmonious cooperation can come about. One way is for harmonious complexes to be favoured by selection over dis-harmonious complexes. The other is for separate parts of complexes to be favoured in the presence, in the population, of parts with which they happen to harmonise." pg 242

"For a nuclear gene to control the shape of the cell in which it sits is presumably simpler than to control the shape of some other cell, or of the whole body in which the cell sits. Yet we conveniently lump the three together and call them all genetic control of phenotype. My thesis has been that the slight further conceptual step outside the immediate body is a comparatively minor one." pg 247

14. Rediscovering the Organism.

After all this there really is something pretty impressive about individual organisms

The minimum unit of replication is about 50 cistrons
Each cell in a eukorite has a complete set of DNA because it is easy

Reproduction is distinguished from growth by the organism being build anew from the basic gamet rather than simple cell division. This is the distinction between meiosis and mitosis – between germ-line cell division and somatic or 'dead-end' cell division.

"Evolution of a complex body structure with organs ... is only possible if there is a cyclical repeating developmental process to evolve." pg 257.

"The importance of the difference between growth and reproduction is that each act of reproduction involves a new developmental cycle. Growth simply involves swelling of the existing body.

Further Reading.

- Pg 113, Dawkins 1976b
- pg 175, Barlow 1961 – discussion of reversible and irreversible codes.
- Pg 251 Simon (1962) – The architecture of complexity
- pg 256, Bonner T J (1974) On Development.
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