Often, multiple traits can be selected in ‘coordinated’ ways in response to common or widely experienced sets of selective ‘forces. For example, in a species that experiences an unstable, rapidly varying resource environment (OR, similarly, inhabits an environment that exists in shifting or short-lived ‘patches’), selection might tend to favor traits like good dispersal ability, rapid growth, early sexual maturity, reproduction in ‘bursts’ with lots of offspring at a time but not much investment in each, and a relatively short overall lifespan. All of these would enhance fitness by optimizing use of resources when they are abundant – and optimizing getting to patches of good resource availability when they become available.

Such coherent assemblage of traits are often referred to as ‘life-histories’. The one just described is often referred to as an ‘r-selected life-history’ – i.e., it optimizes population growth potential (related to ‘r’).

While a species that experiences a predictably stable resource environment over many generations, so that populations typically are near carrying capacity and experiencing intense competition, are likely to be ‘selected for’ traits that enhance competitive ability (i.e., enhance fitness through making them better at competing for resources and reproducing successfully when resources are limited). These might include things like lots of parental care, long life-spans with multiple reproductive events, few offspring at a time but lots of resources invested in each, slow growth, etc. This sort of assemblage of traits is often referred to as a ‘K-selected’ life-history. (Albatrosses live up to a century, lay one big egg every couple of years, etc…)

DANDELION
Leontodon taraxacum L.
CHICORY FAMILY

A dandelion is a good example of an ‘r-selected’ plant. This is equivalent to a ‘weedy’ life history.

Beech trees are good examples of K-selected (‘competitive’) plants (long-lived, slow-growing, big seeds…)

“K-selected” and “r-selected” aren’t absolutes; it’s probably best to think of them as the end points of a gradient/continuum of life-histories. There are also other coherent ‘life-history strategies’ that recur (for example, ‘stress-tolerators’).

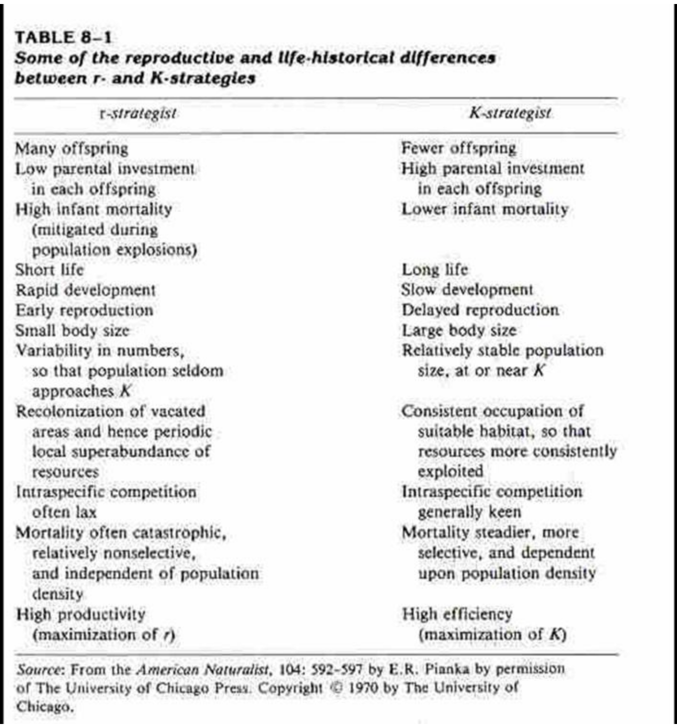
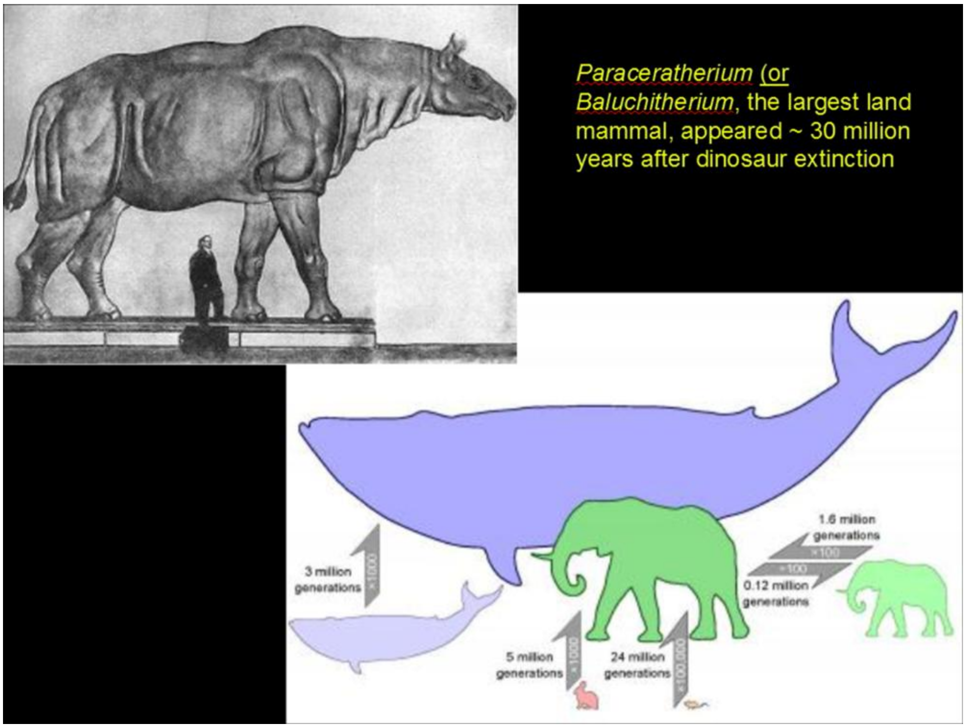


TABLE 8–1

Some of the reproductive and life-historical differences between r- and K-strategies

r-strategist	*K-strategist*
Many offspring	Fewer offspring
Low parental investment in each offspring	High parental investment in each offspring
High infant mortality (mitigated during population explosions)	Lower infant mortality
Short life	Long life
Rapid development	Slow development
Early reproduction	Delayed reproduction
Small body size	Large body size
Variability in numbers, so that population seldom approaches K	Relatively stable population size, at or near K
Recolonization of vacated areas and hence periodic local superabundance of resources	Consistent occupation of suitable habitat, so that resources more consistently exploited
Intraspecific competition often lax	Intraspecific competition generally keen
Mortality often catastrophic, relatively nonselective, and independent of population density	Mortality steadier, more selective, and dependent upon population density
High productivity (maximization of r)	High efficiency (maximization of K)

Source: From the *American Naturalist*, 104: 592–597 by E.R. Pianka by permission of The University of Chicago Press. Copyright © 1970 by The University of Chicago.



Paraceratherium (or *Baluchitherium*, the largest land mammal, appeared ~ 30 million years after dinosaur extinction

Size is another central theme in thinking about life-histories and trade-offs. Being big carries certain advantages (think about competition, avoiding predators, being able to travel large distances, attracting mates), and there's some suggestion that lineages (families, orders…) will tend to show evolution in at least some members towards larger size over evolutionary time. BUT being big may also carry some significant costs (think about resource requirements per individual, time to mature, adaptability if conditions deteriorate). It's also been suggested that, over time, selection will tend to 'drive' an evolutionary line towards increased specialization (like large size), but that increased specialization enhances chance of extinction! Does evolution by natural selection over the 'short' term produce biotic instability over the (very) long term – i.e., turn-over in biota?

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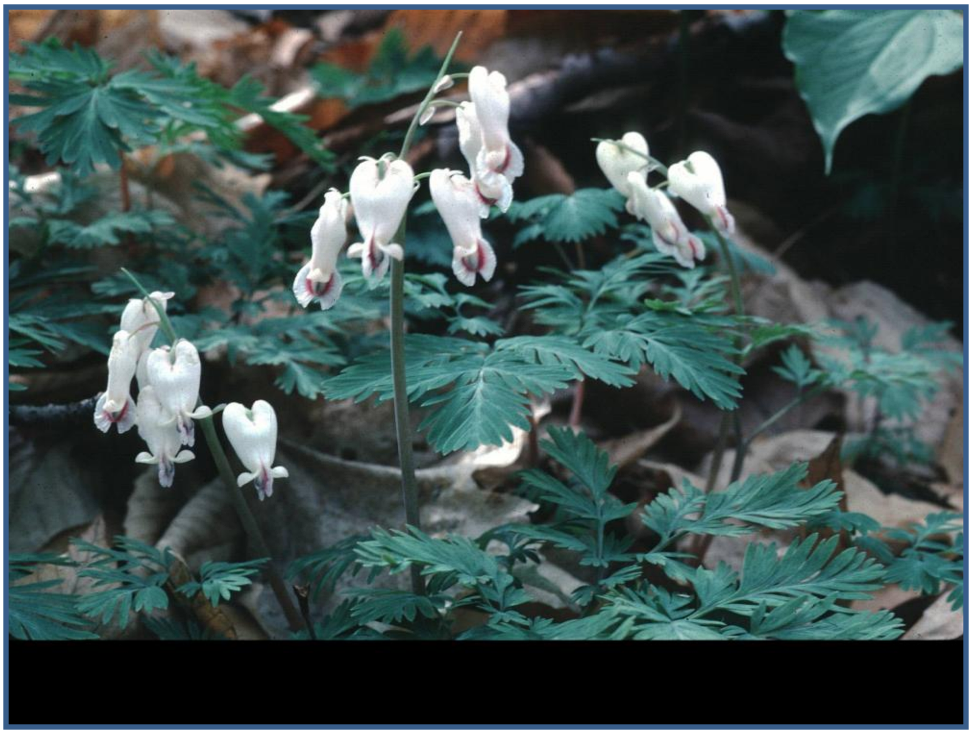
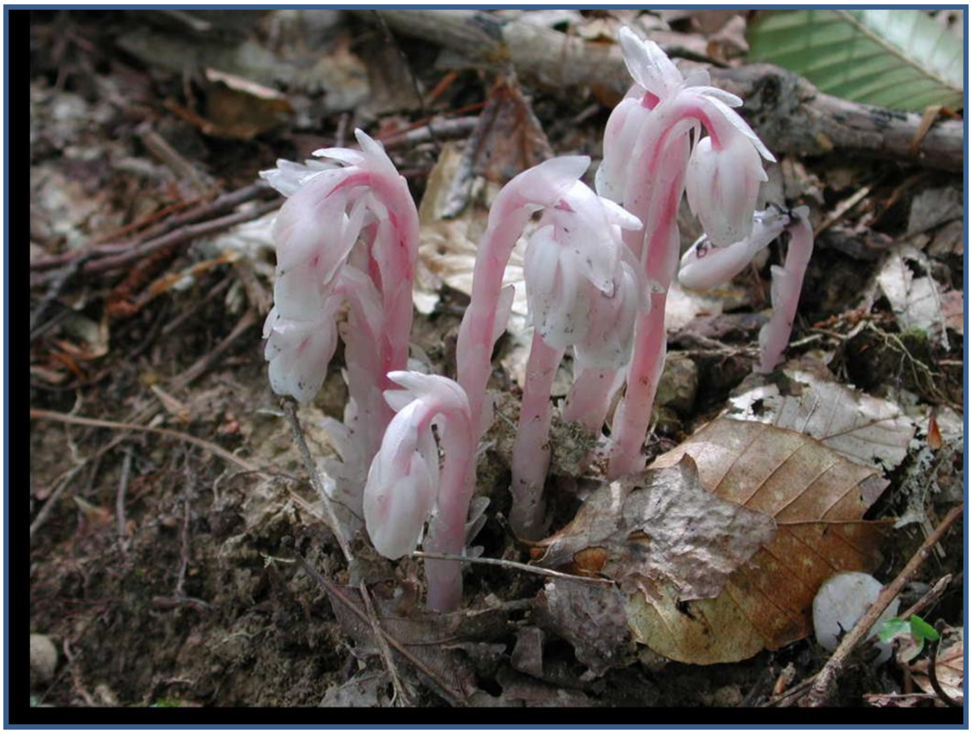


"Simple" natural selection is only the beginning: Darwinian evolutionary theory leads to insights in much more complex scenarios. CO-EVOLUTION refers to situation where the selective regimes for two different species interact so that there is 'feedback'. ALL organisms experience some degree of coevolution, but some cases are particularly prominent and specific. Plant-pollinator systems are a particularly wide-spread and important example of coevolution. They are generally thought of as mutualisms – both parties experience positive, population-level effects. However, selection typically acts on each party to minimize the costs to that party and maximize the benefits. Nectar is expensive, so selection should favor plants that produce the minimum amount necessary to ensure pollination. Selection should act on the ‘pollinator’ to maximize foraging efficiency for nectar regardless of effectiveness with which it pollinates the plant (which would have no effect on ‘pollinator’ fitness). Indeed, many types of insects have evolved means of accessing nectar by means that don’t pollinate the plant at all (you may be able to see the small holes chewed in the upper lobes of some of these flowers; that’s where the nectar glands are located)

Coevolution between plants and pollinators can often produce very precise matches and absolute mutual dependencies. If either party were to be lost from the system, the other would likely be very vulnerable to extinction. In other words, selection can actually enhance vulnerable to extinction through ‘over-specialization’.

And some plants don't reward the pollinator in any way at all; dark brown or red-brown flowers often emit the odor of decaying flesh and attract flies that normally lay eggs on dead animals. There is no food for the fly (or it's larvae); if the fly actually lays eggs at the flower (they do in some cases), this is actually a fitness *cost* since those offspring die. The plant is a parasite on the insect. In this case, it's easy to see the selective benefit to the plant (scents are cheaper than nectar; more energy left for growth and seed production). But it seems that selection ought to favor insects who can be discriminating and avoid this cost. Why do the flies still come to the flower?

This is an orchid that mimics a female bee, even emitting sex pheromones. Male bees copulate with the flower and transfer pollen in the process. Again, the plant is parasitic on the insect. Are these kinds of relationships likely to be stable – i.e., would selection favor their maintenance? There are lots of similar stories.



COEVOLUTION can lead to even more complicated and interesting dynamics. Indian-pipe is a flower plant that lacks chlorophyll; it acquires sugars from a fungal associate rather than from its own chlorophyll. There is no evident benefit to the fungus which is *mycorrhizal* – that is, it lives in association with tree roots and draws its own sugars from green plants. So Indian-pipe is parasitic on the fungus-greenplant mutualism. Consider why selection would predictably lead to selective loss of chlorophyll in such a case. But shouldn’t there be selection on the fungus to somehow ‘reject’ the Indian-pipe’s parasitism? Or is its draining of resources too trivial in relation to the availability of sugars from the tree roots to matter much? Or is Indian-pipe somehow able to evade any ‘rejection’ by the fungus (maybe it looks too much like the roots of photosynthetic plants for the fungus to differentiate? Action of selection in the interplay between parasites and predators and their hosts or prey is an intensive area of study.

When parasites/predators are introduced to a system where they didn't previously exist – where there is no history of coevolution – results can be unpredictable and often problematic. White-nose syndrome is caused by a fungus infecting North American bats, and it can be highly lethal. The fungus was introduced recently from Europe; North American bats have no coevolved tolerance of the microorganism. IF any resistance were to occur among local bat populations (either due to a rare existing genetic trait or a new mutation), even if it's only modest, one would expect to have a very large effect on fitness, and to spread rapidly through the bat population. (This may actually be happening.) Most of the environmental 'issues' associated with invasive species may be associated with the 'breakage' of coevolved relationships.

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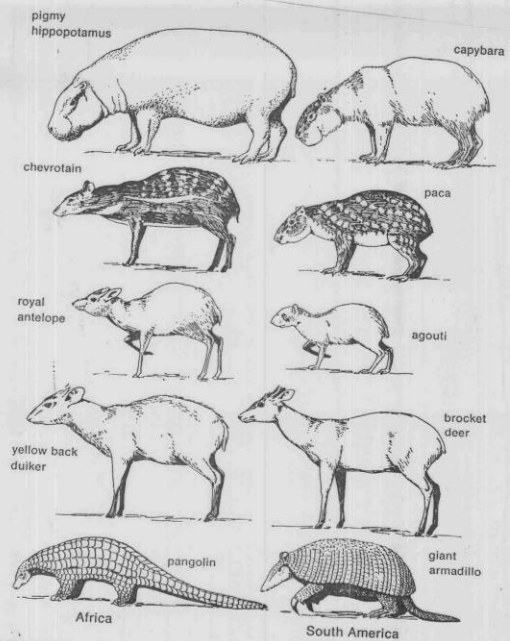
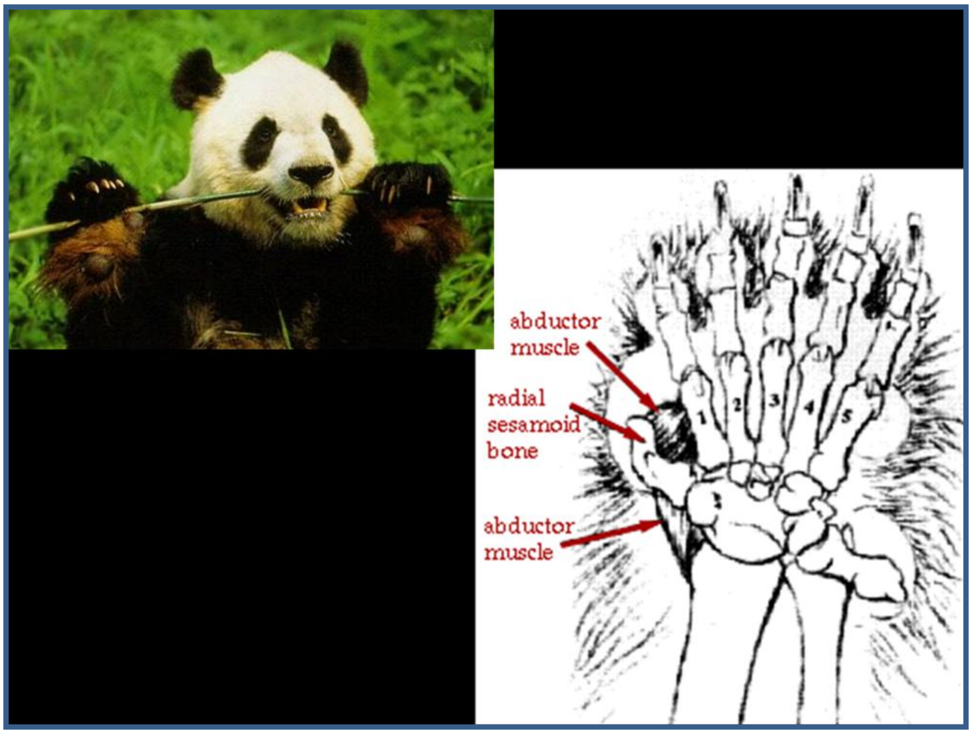


FIGURE 17–12 Morphological convergence among unrelated African (left) and Neotropical (right) rain-forest mammals. Each pair of animals is drawn to the same scale.

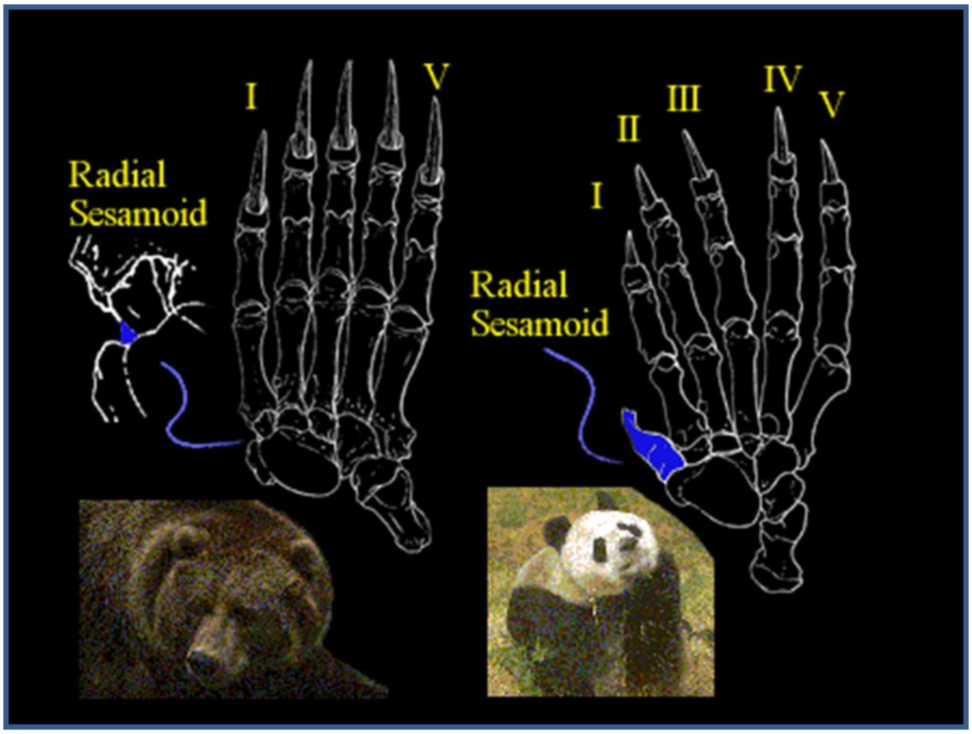
Another interesting broad-scale evolutionary phenomenon is CONVERGENCE: Just as the ‘tree-things’ in the earlier story (and real trees) seem to find similar solutions to the general problems of being a plant, there are patterns in all groups of organisms where ‘solutions’ seem to crop up repeatedly. This suggests that there are simply some ‘good ways’ of doing certain things – of making a living – and they’re hit on repeatedly. The result is often referred to as ‘convergent evolution’. The pairs of mammals shown here are ecological analogues, but from different continents, and from different families (so not closely related).

But convergence if often imperfect. The elegantly adapted true woodpeckers – organic jackhammers – are completely ineffective at dispersing across water (a trade-off!), and they never occur on oceanic islands. Where there are no true woodpeckers, convergent evolution has produced adaptations in other birds that allow use of some of the same resources, but none are as efficient/effective. Selection can't always be counted on to 'find' the most effective or elegant solution to a problem. The variations that provided the selective path to 'woodpecker-ness' may not have been available in the right sequence or at all. (Upper right is the Galapagos 'woodpecker finch' that uses a cactus thorn the way a true woodpecker uses its beak – it is a tool-using bird; lower right is a New Zealand species, now extinct, where mated pairs used sexually dimorphic beaks to pry and probe for wood-dwelling insects through cooperative foraging.)

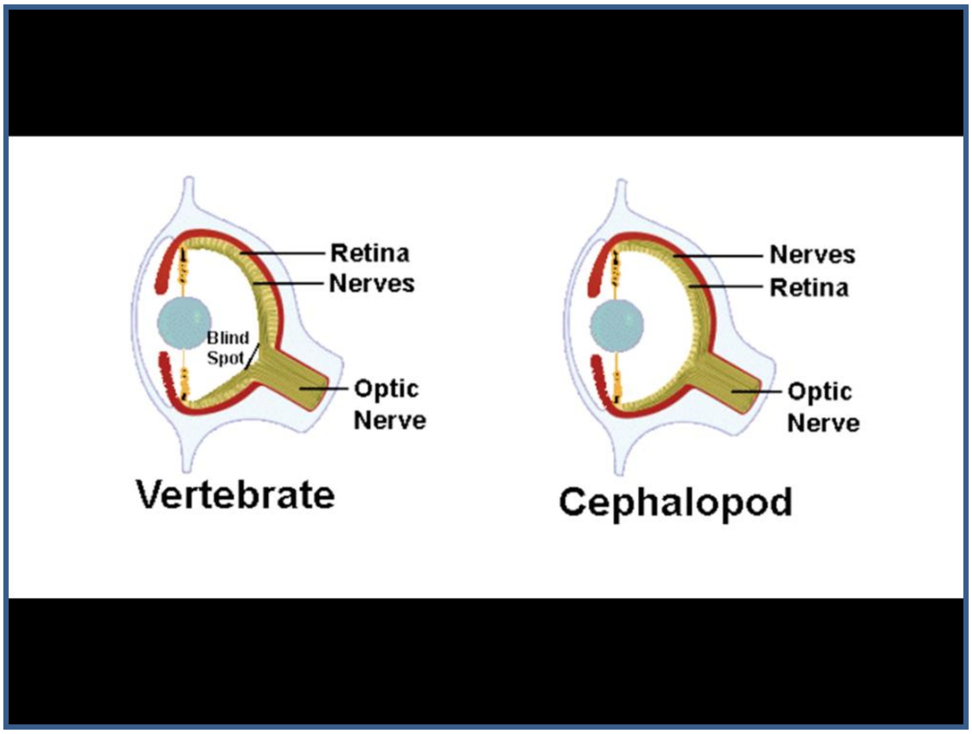
Hummingbirds (new world only) are convergent with sunbirds (old world) in many ways – but there are differences; sunbirds can’t hover. Their coevolved plants show corresponding differences. Though both tend to have red flowers, the old world plants must provide perches (which also makes their flowers more accessible to non-coevolved nectar 'thieves' who might not be effective pollinators) . These examples point to some important CONSTRAINTS ON EVOLUTION BY NATURAL SELECTION. The 'solutions' achieved by natural selection to a particular problem may not be the best POSSIBLE solutions; they need only be better than any other solutions that have been available in the particular environment/population.



Another illustration of how the mechanism of selection leads to imperfect and/or unexpected or odd results. The ‘panda’s thumb’ – actually an enlarged wrist bone – is not a very ‘good’ thumb (no joints, not very strong or flexible), but pandas with this poor excuse for a thumb can still strip bamboo faster than pandas without – and there is no variation within the panda gene pool that allows selection to favor ‘opposability’ of one of the true fingers.



This is an example of a ‘phylogenetic constraint’. Pandas are descended from a bear ancestor; bear paws have an already-enlarged radial sesamoid bone with some muscularization, but don’t offer gripping by true digits..



Another phylogenetic constraint: vertebrate eyes have a ‘blind spot’ because the retina is interrupted by the optic nerve passing *through* it, and the nerves that connect to rods and cones actually pass over the front of the retina – a really bad design, presumably a result of early stages of eye evolution ‘locking in’ this basic structure. We compensate in various ways, but there’s no pathway of incremental variations by which selection could now ‘correct’ this design flaw. Cephalopod (octopus, squid) eyes have the ‘right’ wiring design (but they lack an adjustable lens; they focus by changing the shape of the whole eyeball).

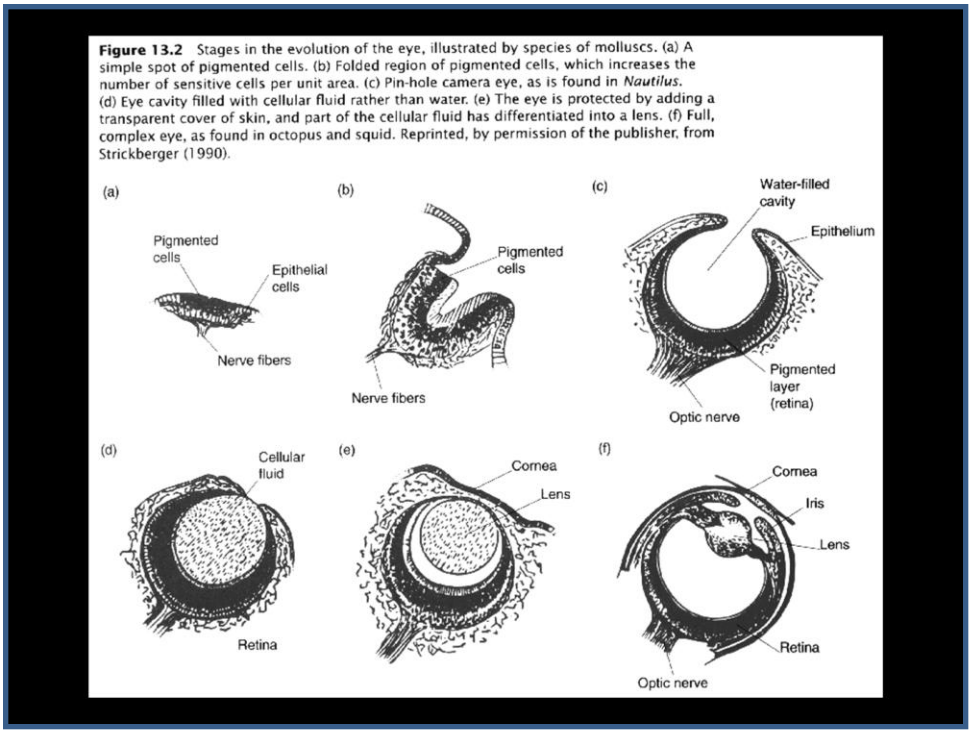
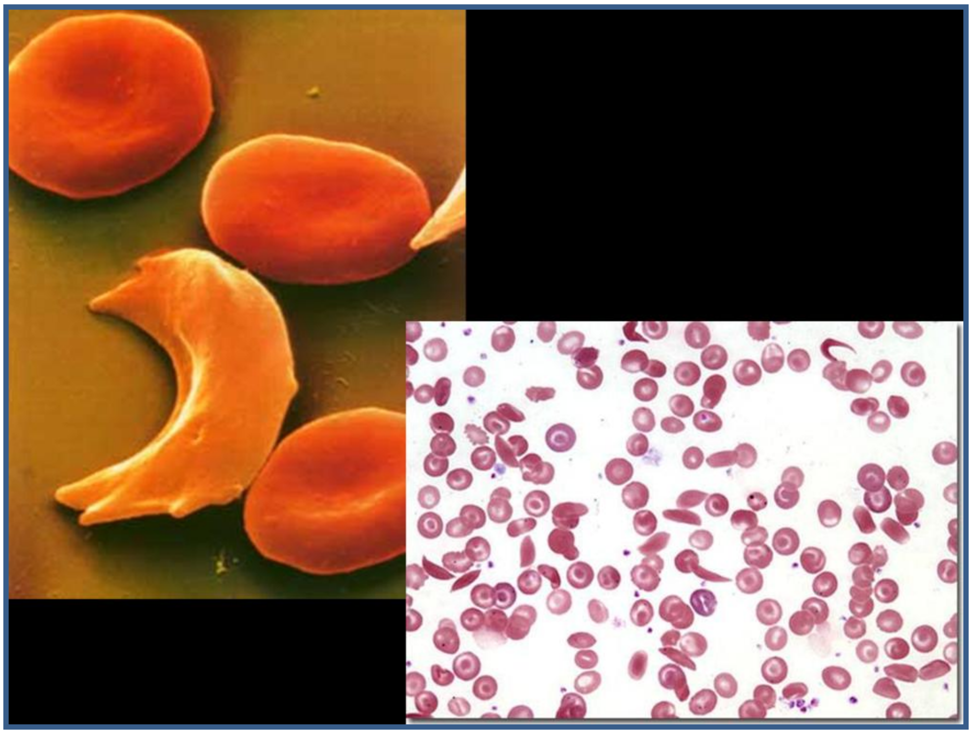
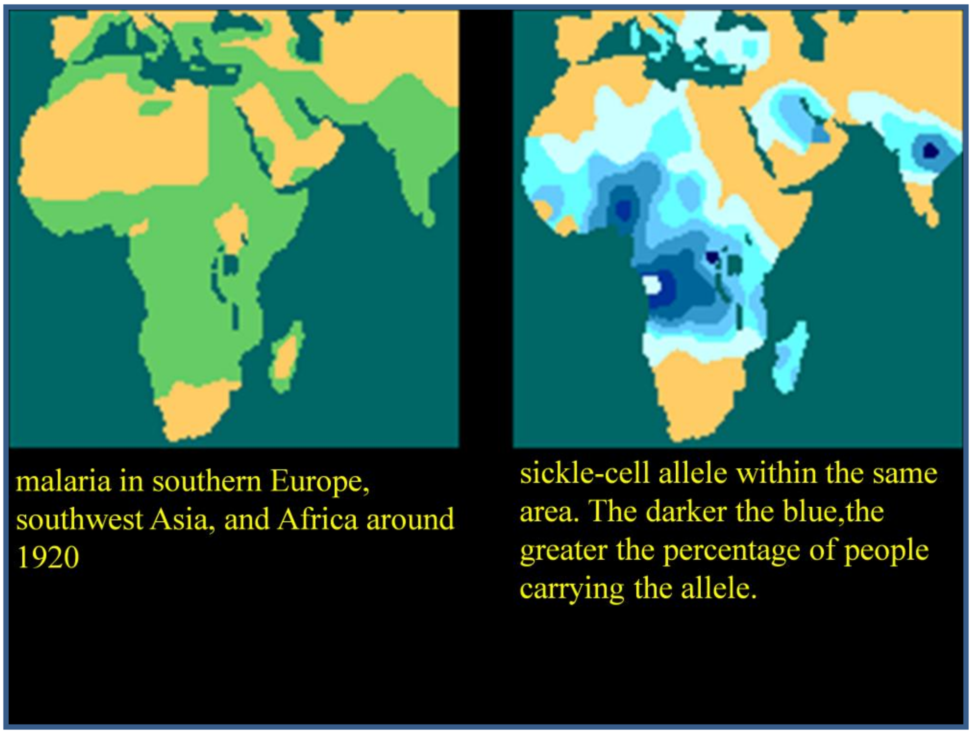


Figure 13.2 Stages in the evolution of the eye, illustrated by species of molluscs. (a) A simple spot of pigmented cells. (b) Folded region of pigmented cells, which increases the number of sensitive cells per unit area. (c) Pin-hole camera eye, as is found in *Nautilus*. (d) Eye cavity filled with cellular fluid rather than water. (e) The eye is protected by adding a transparent cover of skin, and part of the cellular fluid has differentiated into a lens. (f) Full, complex eye, as found in octopus and squid. Reprinted, by permission of the publisher, from Strickberger (1990).

A side-line story concerning eye evolution. Selection generally acts on incremental variations (think about the 'tree-thing' story) – radically different end points are only achieved by accumulation of small changes over many generations. Some 'evolution-skeptics' have argued that complex structures like eyes can't come about by small changes because 'intermediate' forms would not work; this is sometimes referred to as the argument from 'irreducible complexity'. There are several answers to this argument (which is, in fact, less of an argument than a statement of faith). For example, remember that the 'intermediate' forms only have to work *better* than anything else that's around at the time; they aren't required to work as well as the current 'end-product'. 'Half an eye' would not work, claim the critics. But, in fact, a poorly functioning eye (half an eye) is a lot better than none. These are all forms of light-sensing organs that occur in living organisms somewhere; they form an incremental series from a patch of pigmented cells to a fully functional vertebrate eye. (Note that a simple light-sensitive 'pit' as in (b) will allow sensing of the direction from which light is coming). It is also possible that 'complex' structures developed for different 'uses' and have been 'converted'; feathers began as scales…



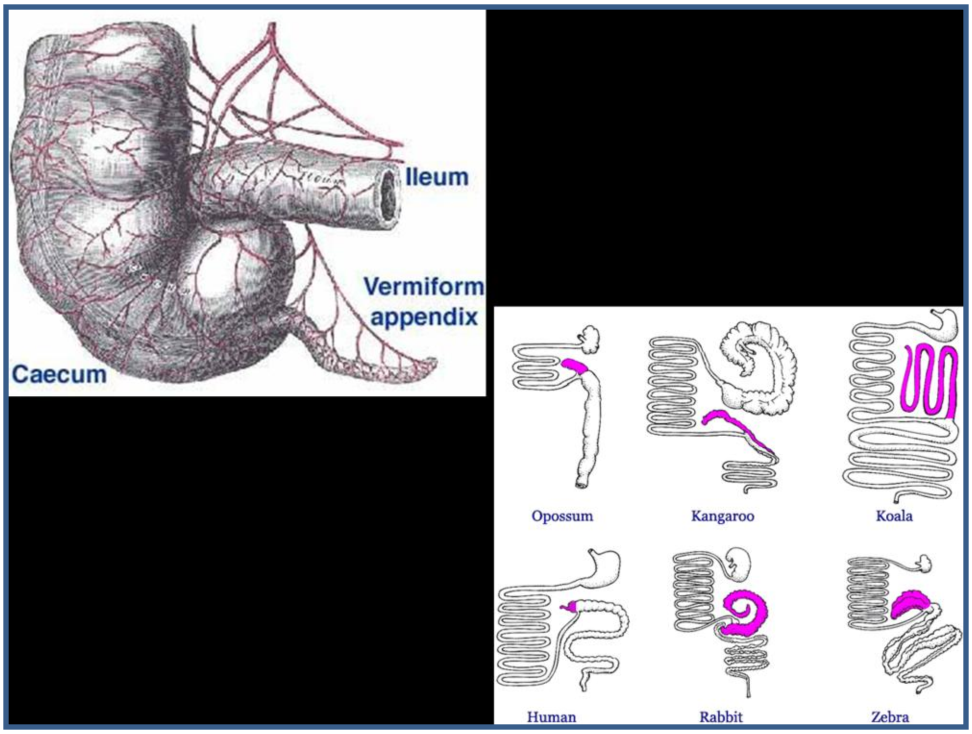
Another 'sub-optimal' selective solution: The sickle-cell trait – a simple recessive mutation of the hemoglobin gene in humans – causes a tendency to anemia by causing red blood cells to be sensitive to stress (they collapse into ‘sickle’ form and become nonfunctional). In homozygote condition (two copies of the gene), carriers almost always die in childhood. In heterozygote form (one copy of the mutation, one ‘normal’ copy of the gene), the tendency to anemia is relatively mild, but the carrier is resistant to malaria, a disease that has killed vast numbers of people before reproductive age. This amounts to an extreme selective 'trade-off' that only enhances fitness when the penalty of not having the trait is really large…



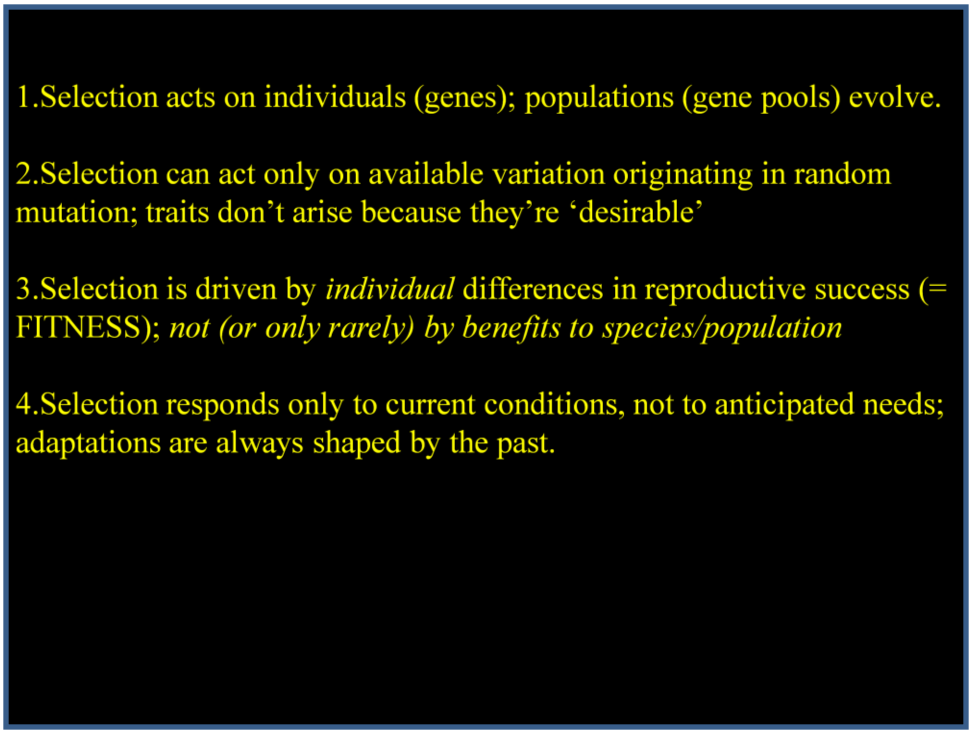
malaria in southern Europe, southwest Asia, and Africa around 1920

sickle-cell allele within the same area. The darker the blue,the greater the percentage of people carrying the allele.

Despite its great fitness cost to carriers – on average, a quarter of the children of two ‘carrier’ parents will die in childhood due to sickle-cell anemia – the sickle-cell gene is prevalent throughout the region where malaria is endemic. Reduction of one large fitness cost more than compensates for the other. A design trade-off that illustrates that natural selection is not always an ‘efficient’ designer -- a good design would be resistance without such a huge trade-off – but selection can only work with the variations available from mutation.



Another example of constraints on selection: The human appendix is a costly organ; it’s not functional in humans, but can cause sickness and death if infected. Why hasn't selection eliminated it? The homologous organ functions as a digestive aid in other mammals that eat low-quality foliage. Selection in humans, specialists in ‘high-quality’ food (fruits and meat), has reduced the organ to a ‘vestigial’ state. Why isn’t it altogether eliminated, reducing the selective costs of appendicitis? Perhaps it’s because an even smaller appendix actually increases risk of appendix – so any small change in appendix size leads to lower fitness (stabilizing selection), even though a *large* developmental change (to no appendix) would be great, it's not something likely to occur spontaneously…



1.Selection acts on individuals (genes); populations (gene pools) evolve.

2.Selection can act only on available variation originating in random mutation; traits don’t arise because they’re ‘desirable’

3.Selection is driven by *individual* differences in reproductive success (= FITNESS); *not (or only rarely) by benefits to species/population*

4.Selection responds only to current conditions, not to anticipated needs; adaptations are always shaped by the past.

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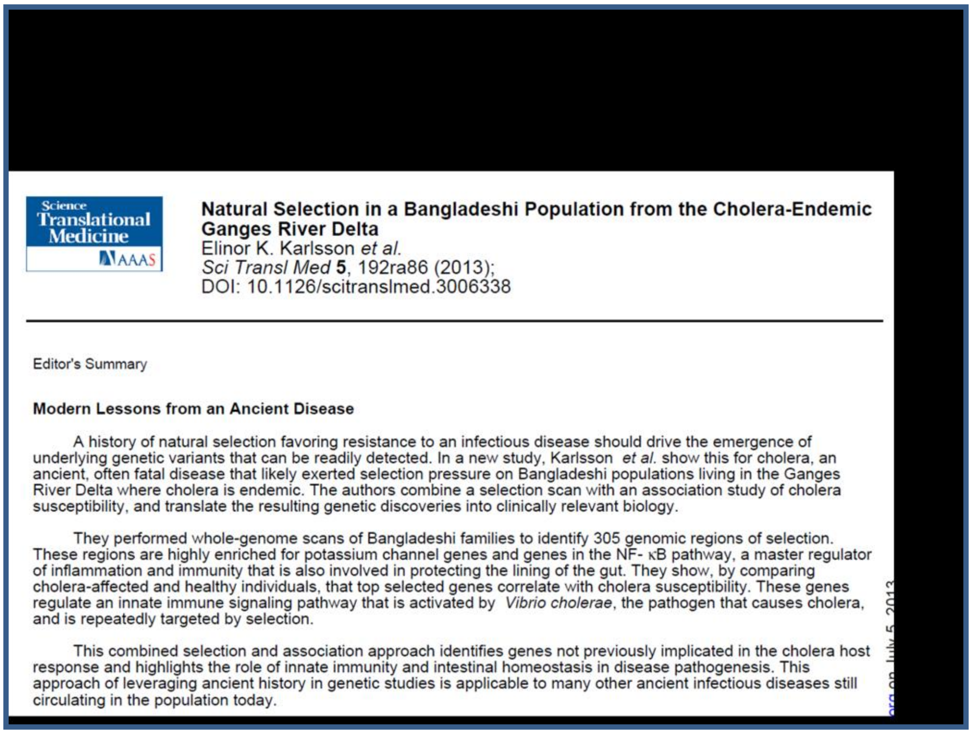


Science Translational Medicine AAAS

Natural Selection in a Bangladeshi Population from the Cholera-Endemic Ganges River Delta

Elinor K. Karlsson *et al.*

Sci Transl Med **5**, 192ra86 (2013);

DOI: 10.1126/scitranslmed.3006338

Editor's Summary

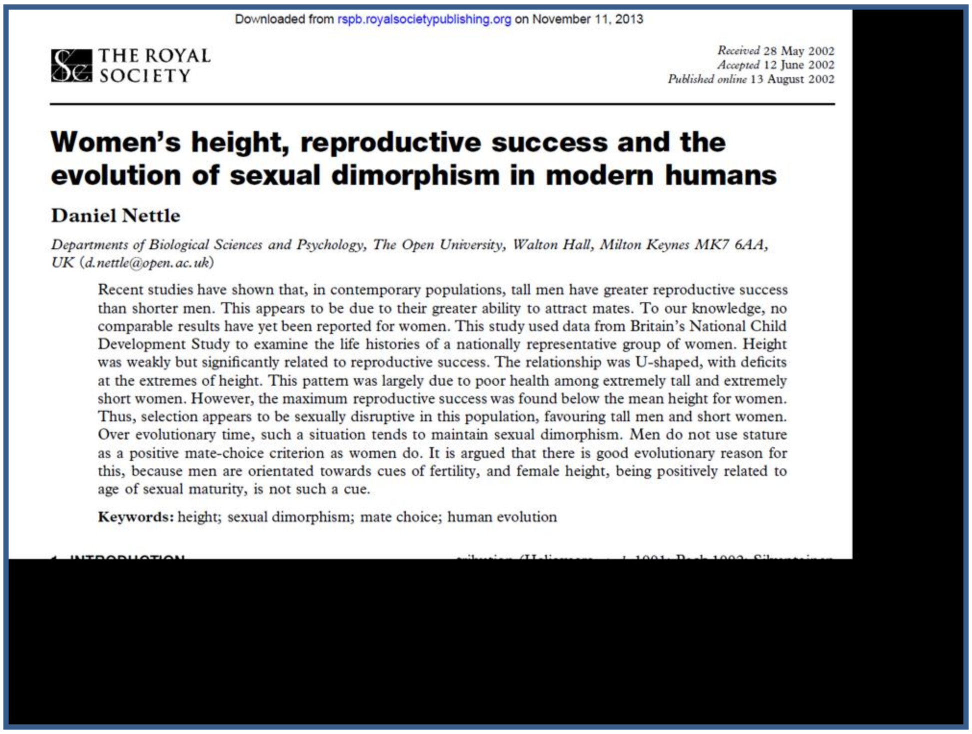
Modern Lessons from an Ancient Disease

A history of natural selection favoring resistance to an infectious disease should drive the emergence of underlying genetic variants that can be readily detected. In a new study, Karlsson *et al.* show this for cholera, an ancient, often fatal disease that likely exerted selection pressure on Bangladeshi populations living in the Ganges River Delta where cholera is endemic. The authors combine a selection scan with an association study of cholera susceptibility, and translate the resulting genetic discoveries into clinically relevant biology.

They performed whole-genome scans of Bangladeshi families to identify 305 genomic regions of selection. These regions are highly enriched for potassium channel genes and genes in the NF- κB pathway, a master regulator of inflammation and immunity that is also involved in protecting the lining of the gut. They show, by comparing cholera-affected and healthy individuals, that top selected genes correlate with cholera susceptibility. These genes regulate an innate immune signaling pathway that is activated by *Vibrio cholerae*, the pathogen that causes cholera, and is repeatedly targeted by selection.

This combined selection and association approach identifies genes not previously implicated in the cholera host response and highlights the role of innate immunity and intestinal homeostasis in disease pathogenesis. This approach of leveraging ancient history in genetic studies is applicable to many other ancient infectious diseases still circulating in the population today.

Another common misconception about evolution: “Modern medicine has ended selection on humans”. Simply untrue, and lots of evidence to the contrary…



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Women's height, reproductive success and the evolution of sexual dimorphism in modern humans

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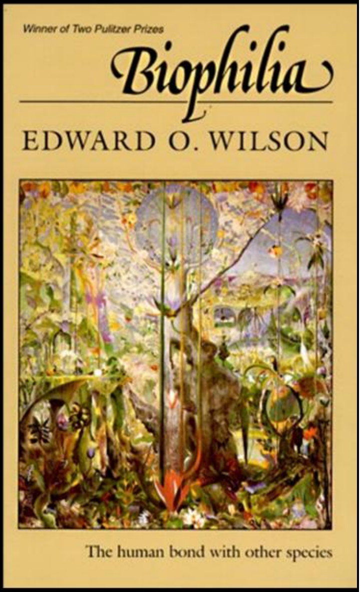
Recent studies have shown that, in contemporary populations, tall men have greater reproductive success than shorter men. This appears to be due to their greater ability to attract mates. To our knowledge, no comparable results have yet been reported for women. This study used data from Britain's National Child Development Study to examine the life histories of a nationally representative group of women. Height was weakly but significantly related to reproductive success. The relationship was U-shaped, with deficits at the extremes of height. This pattern was largely due to poor health among extremely tall and extremely short women. However, the maximum reproductive success was found below the mean height for women. Thus, selection appears to be sexually disruptive in this population, favouring tall men and short women. Over evolutionary time, such a situation tends to maintain sexual dimorphism. Men do not use stature as a positive mate-choice criterion as women do. It is argued that there is good evolutionary reason for this, because men are orientated towards cues of fertility, and female height, being positively related to age of sexual maturity, is not such a cue.

Keywords: height; sexual dimorphism; mate choice; human evolution



Winner of Two Pulitzer Prizes

Biophilia

EDWARD O. WILSON

The human bond with other species