Overview of Lecture: Adaptation & Imperfection
Read: Text pgs 450-451, ch 22 & 23
We’ll consider what it means to say a trait is an adaptation, why adaptations aren’t “perfect” (and why it matters)

Bullet Points:
• What is an adaptation?
• Current function - current selection
• Past selection, independent convergences
• Cats and sweets
• Constraints to perfection
• Correlations and tradeoffs
• Time lags and the Environment of Evolutionary Adaptedness EEA
• Gene flow
• Coevolution and the red queen

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 comes into competition. And we see that this is the standard of perfection attained under nature.
Darwin, C. R. 1872. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. 6th edition
CHAPTER VI. DIFFICULTIES OF THE THEORY. pg 163
We want to keep evolutionary biology ‘scientific,’ avoiding un-testable ‘Just So Stories’ about how “everything is adaptive in this best of all possible worlds!”

How can tell if a trait is ‘adaptive?’

We want to keep evolutionary biology ‘scientific,’ avoiding un-testable ‘Just So Stories’ about how “everything is adaptive in this best of all possible worlds!”
“The result of natural selection is **evolutionary adaptation.**”

So, what do we mean by an **adaptation**? \{product (noun) vs process (verb)\}

1. An adaptation -

Test w/ **experimental manipulation** of phenotype and/or pheno-env ‘match’
- see if alternatives perform worse, & why

Is male tail length
‘an adaptation to’
(under current selection by)
aerodynamics, or
to attract females?

**a false dichotomy**

- Shorten:
- Lengthen:

**Fitness depends on survival and reproduction.**
Conflicting effects of tail length on survival and repro create a fitness tradeoff – stabilizing selection.

The phenotypic trait **tail length**
doesn’t ‘perfectly’ max either survival or reproduction;
it’s a compromise that **maximizes fitness by balancing a tradeoff.**
2. An adaptation

More demanding,

Past history is not amenable to experimental manipulation, but short-term ‘future history’ is

(a) Artificial selection shows ‘history in progress’ - adapt to farm, hospital & lab

(b) “Natural experiments” show ‘recent history’: fluctuating selection on beaks in Galapagos finches:

(c) Phylogenetic methods allow us to infer the history of traits (text ch 25); Compare across natural differences: look for patterns of
Cats lack a sweet tooth.

Genetic analysis explains pets' indifference to sugary treats.

On most mammalian tongues, specialized taste bud receptors pick up on sweet tastes and send a pleasant signal to the brain. The receptors contain a pair of proteins called T1R2 and T1R3 ... that ultimately signal a sweet sensation.

Scientists first documented cats' behavioural indifference for sugar in the 1970s. But no one could explain why proximate domestic cats couldn't care less about candy. J. Brand and colleagues sequenced the regions of the domestic cat's DNA that code for the T1R2 and T1R3 proteins.

Genes that are not important for a species' survival tend to accumulate more mutations over time, according to Brand. As cats are strict carnivores, they may have had no use for tasting sugar, he suggests.

Analyses of Sweet Receptor Gene (Tas1r2) and Preference for Sweet Stimuli in Species of Carnivora. Li X, et al. 2009 J. Heredity100:S90-S100. {same for other cats}

{So, is the loss of sugar receptors in carnivorous cats an ‘adaptation’?}
Carnivores pick meats over sweets

Meat-eating animals

An animal with a diet devoid of vegetables may have little need to detect sugars … parallels with cave-dwelling fish that have lost their sense of sight. Most mammals {have} taste receptors that detect salty, sour, sweet, bitter and savoury foods.

To see whether other carnivores also lack sweet receptors, Jiang et al. collected DNA …

Seven species contained a broken … Tas1r2 …

That the mutations are not identical across species suggests that carnivores have independently lost their ability to detect sugars … convergent evolution.

There is no evidence, however, that carnivores benefit from losing the ability to sense sugars, … {but… }
Adaptations are ‘better’ than random but not perfect.

Why aren’t organisms perfect?

There are various kinds of constraints to evolution:
http://evolutionwiki.org/wiki/Constraints_on_perfection

A. You-can’t-get-there-from-here:

(valleys in adaptive landscape)

B. You-didn’t-really-want-to-anyway:

as with swallow tail feathers: ‘perfect’ aerodynamics wouldn’t max fitness

C. You-can-but-it-will-take-time-&-luck:

1. Chance: selection only operates on existing variation; depends on chance (or ‘engineered) mutations, drift & quirks of history. (A1)

(Note: ‘perfect’ is ill-defined - what is best possible anyway?)
Genetic correlations: Side-effects & tradeoffs

The trade-off between number and size of offspring in humans and other primates

Life-history models assume that parents make investment "decisions" that maximize expected reproductive success (fitness) in the face of constraints whereby energy, effort, resources or time invested in the provisioning of current offspring cannot be invested in producing more future offspring.

As a consequence,

one of the life’s most fundamental trade-offs is between:

... to our knowledge no attempt has been made to uncover the trade-off between number and size of offspring across human societies ...

provided an adjustment is made for mother’s energy budget \{1/\text{Mass}^{3/4}\}.

{ any possible confounding variables? }
Genetic correlations: Side-effects & tradeoffs

Senescence (aging) - the great ‘imperfection’

(in jargon: a negative or antagonistic pleiotropic genetic effect).

a) a bird in the hand … you can’t reproduce after accidental death
b) early repro worth more because offspring repro sooner
   - like compound interest.

You can select for longevity in fruitflies & get correlated reduction in early reproduction.

Artificial selection on male longevity
influences age-dependent reproductive effort

in the black field cricket ... Hunt et al. 2006. Am Nat 168, 3 E-Article

We selected directly on adult longevity of male field crickets
and measured the correlated responses of age dependent reproductive effort ...

Males from downward selected lines

Our findings directly support the antagonistic pleiotropy model of aging
and suggest an important role for sexual selection in the aging process.
Grandmother Hyp: women evolved menopause (early cessation of repro) and longer post-repro life (alternatively: menopause is a non-adaptive artifact of recent increase in longevity)

Fitness benefits of prolonged post-reproductive lifespan in women

Using complete multi-generational demographic records, we show that women with a prolonged post-reproductive lifespan and hence greater fitness, in pre-modern populations of both Finns and Canadians. This fitness benefit arises because post-reproductive mothers enhance the lifetime reproductive success of their offspring by allowing them to breed earlier, more frequently and more successfully. …

See: The Grandmother Effect
Lachmann, P.J. 2011. GERONTOLOGY 57:375-377

Thank Grandma for Longevity
2012 Nature 491, 162
Conflict between women and their daughters-in-law could be a factor in explaining an evolutionary puzzle - the human menopause. 

Humans, pilot whales and killer whales are the only animals known to stop being able to reproduce long before they die. In terms of evolution, where passing on your genes is the main reason for living, the menopause remains puzzling.

Lahdenperä et al. (Ecology Letters 2012) … used data from meticulous birth, death and marriage records kept by the Lutheran church in Finland between 1702 and 1908.

For children of the older women, survival dropped by 50%. For children of the daughters-in-law, it dropped by 66%. However, if mothers and daughters {not daughters-in-law} had children at the same time,
Gene Called Link Between Life Span and Cancers

NICHOLAS WADE  Sept 7, 2006

Biologists have uncovered a deep link between life span and cancer in the form of a gene {p16-Ink4a} that switches off stem cells as a person ages. The critical gene, well known for its role in suppressing tumors, seems to mediate a profound balance between life and death. It weighs the generation of new replacement cells, required for continued life, against the risk of death from cancer, which is the inevitable outcome of letting cells divide.

To offset the increasing risk of cancer as a person ages,

The finding suggests that many degenerative diseases of aging are caused by an active shutting down of the stem cells that renew the body’s various tissues and are not just a passive disintegration of tissues under daily wear and tear.

The evolutionary purpose is evidently to avert the risk that

Ageing: Balancing regeneration and cancer

CM Beausejour & J Campisi

NATURE|Vol 443|28 September 2006

The proliferation of cells must balance

{a negative tradeoff constraint}
Schizophrenia genes 'favoured by evolution' published online: 5 September 2007
... a survey of human and primate genetic sequences ... (Crespi et al. 2007. PRSLB)
suggests that genes linked to the debilitating brain condition conferred some advantage that allowed them to persist in the population — although it is far from clear what this advantage might have been.

Researchers examined 76 DNA sequences linked to schizophrenia.
Of the 76 genes studied, 28... showed less variation than control sequences from elsewhere in the genome, and had less evidence of having been jumbled up by recombination.

These findings suggest that these schizophrenia-linked sequences may have conferred an evolutionary advantage ... stabilizing selection?
The genetic data provide no clues to the kind of advantage that schizophrenia-linked genes might have offered.
Nevertheless, the results might explain why schizophrenia — which can be inherited — has persisted without being stamped out by evolutionary forces.
Some inherited diseases also benefit the person affected, or their kin, or were at least sometimes beneficial in ancestral environments which helps to explain why they have persisted.
The mutation that causes cystic fibrosis protects carriers from cholera.
The mutation behind sickle-cell disease confirs immunity to malaria. [C&R ch 23]

Recent Adaptive Selection at MAOB and Ancestral Susceptibility to Schizophrenia
Dogs have an unusual ability for reading human communicative gestures (e.g., pointing) in comparison to ... chimps or wolves. ... it is unclear whether this evolution is a result of fear and aggression toward humans - as is the case with a number of morphological and physiological changes associated with domestication.

We show here that fox kits from an experimentally domesticated population selectively bred over 45 years to approach humans fearlessly and nonaggressively are not only as skillful as dog puppies in using human gestures but are also more skilled than fox kits from a second, control population not bred for tame behavior (critically, neither population of foxes was ever bred or tested for their ability to use human gestures).

These results suggest that sociocognitive evolution has occurred in the experimental foxes, and possibly domestic dogs, and it is likely the observed social cognitive evolution did not require direct selection for improved social cognitive ability.
Time lags

There is an idea that many human behaviors are anachronistic adaptations to the ‘EEA’ (Environment of Evolutionary Adaptedness) roughly – the pleistocene;


The fundamental assumption of evolutionary psychology is that the human mind is the product of evolution just like any other bodily organ, and that we can gain a better understanding of the mind by examining evolutionary pressures that shaped it.

... why it is that humans struggle with the ideas that immigration and trade can be good things ...
The ‘EEA’: the ‘good old days’ on the savanna

**women:** stay close to home, more verbal & nurturing

**men:** navigate far from home, analyze, use muscle & tools

Adaptation to the EEA is an appealing hyp. for craving for salt, sugar, fat:

Are lawns a grand effort to recreate the EEA?
www.shef.ac.uk/assem/5/chamberl.html

Is aggression a vestige?
-or an artifact?
-http://www.anth.ucsb.edu/chagnon.html

“Men are genetically programmed to select ugly clothing. This dates back millions of years, to when primitive tribal men would deck themselves out in face paint, animal heads and nose bones, so as to look really hideous and scare off enemy tribes.” (5/7/95)

Can evolutionary psychology explain reproductive behavior in the contemporary United States?


... wealthy men nonetheless have more sex partners and ... would have achieved greater reproductive success in the ancestral environment without effective contraception.

*Plausible hypotheses, but until tested, ‘just so stories!’*
Bowling with our imaginary friends
Kanazawa S Evolution and Human Behavior 23 (3): 167-171 MAY 2002

Abstract:

I contend that, because evolved psychological mechanisms have difficulty comprehending entities that did not exist in the environment of evolutionary adaptedness (EEA), humans should fail to distinguish between real friends and the imaginary ones they see on TV.

... analysis of the US General Social Survey (GSS) data indicates that 
... consistent with my contention that the human brain has difficulty distinguishing real friends and people they see on TV, because TV did not exist in the EEA, where every realistic image of someone you repeatedly and routinely saw was your real friend. !?!!!
Gene flow can disrupt local adaptation, resulting in a kind of ‘average’ adaptation that is not ‘perfectly’ specialized to any of the local environments.


Abstract:
... Using blue tits in Mediterranean habitat mosaics ... compares

two isolated landscapes \{mainland, France
island of Corsica

and ... two habitat types \{deciduous
evergreen trees

Deciduous habitats are more common than evergreen habitats on the mainland whereas the opposite is true on the island.
Results suggest that:

(1) on a regional scale, each population is specialized to the more common habitat, i.e. life history traits have evolved in such away that breeding success is high;

(2) in the less common habitats within each landscape, birds are clearly mistimed - they mismatch the best period of food availability, and hence their breeding success is lower; ...
Several important crops have been engineered to express toxins of Bacillus thuringiensis (Bt) for insect control. Bt-transgenic plants can greatly reduce the use of broader spectrum insecticides, but the evolution of insect resistance may hinder this technology.

Present resistance management strategies rely on a "refuge" composed of non-Bt plants to conserve susceptible alleles. The idea/hope/hyp is that the flow of non-resistant genes from these refuges will disrupt the evolution of Bt resistance in the treatment areas.

We have used Bt-transgenic broccoli plants and the diamondback moth as a model system to examine resistance management strategies. … Results indicate that great care must be taken to ensure that refuges … produce adequate numbers of susceptible alleles. Enough gene flow to disrupt local adaptation to Bt!

BT corn is fed to livestock; for more info on genetically modified foods for humans, see: http://en.wikipedia.org/wiki/Genetically_modified_food

Bacillus thuringiensis (Bt) toxins are bacterial proteins that kill some insects and are widely used in crops for pest control. A major concern has been that the pests will develop resistance; refuges, where non-transgenic plants grow next to transgenic plants, have been hypothesized to delay the evolution of resistance because resistant individuals will mate with susceptible individuals from the refuge and hence not confer resistance (if inheritance is recessive) to their offspring. Tabashnik et al. have analyzed field studies from around the world ... They found that resistance has evolved in populations of the corn earworm at some U.S. locations but not at others ... they conclude that the refuge strategy has been successful in slowing the evolution of resistance ...

When a farmer plants a vulnerable refuge and raises “non-resistance genes” instead of corn - who benefits? - who pays the costs?
Clearly, **sex confers some benefit in addition to reproduction**; otherwise, sexual individuals would soon be outcompeted whenever asexual individuals appeared by mutation or migration.

One hypothesis: **the importance of genetic variation in resistance to disease**. Of course, because most pathogens evolve very rapidly … resistance of a particular host genotype to a given disease is not permanent. Biologists call this **coevolution in a host-parasite relationship the "Red Queen effect,“** after the Red Queen in Lewis Carroll’s *Through the Looking Glass*, who admonished Alice that she would have to run as fast as she could to keep from going backward. **{recall the sweaty t-shirt study}**
Maternal versus paternal inheritance of HLA class I alleles among HIV-infected children: consequences for clinical disease progression.


When children acquire HIV infection from their mothers they acquire virus with a history of encounter with maternal HLA {MHC} -mediated immune responses. {the HIV has a history of selection to adapt to (evade) maternal mhc products}

We tested whether time to AIDS diagnosis or death, among a cohort of 59 HIV-infected children in NYC followed from birth for up to 12 years, was associated with maternally- or paternally-inherited child HLA class I alleles, and with HLA similarity between mother and child.

HIV-infected children with an HLA allele usually associated with slow disease experienced a slower progression to AIDS or death only if the allele was paternally inherited. …

If the allele was present in the mother, no association was observed.

CONCLUSION: HLA-mediated selective pressures on the virus in a transmitting mother-infant pair may undermine HLA-mediated viral control in the child.