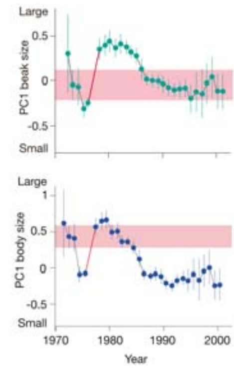
Studying adaptation: tradeoffs in changing environments

Organisms are remarkably able, intricate, and (at least in many cases) beautiful.

Are *all* of their features adaptive? If not, which ones? How can we know?

Is adaptation an ongoing process for most species? Or something from their past?

Beak and body sizes of *Geospiza fortis* on Isla Daphne Major: ongoing evolution by natural selection



Beak size and body size increase dramatically in response to the drought of 1977, but both then decrease slowly.

Adaptation to the tradeoff:
Larger beaks and bodies are favored when most seeds are large and hard;
smaller beaks and bodies are favored when most seeds are small and soft.

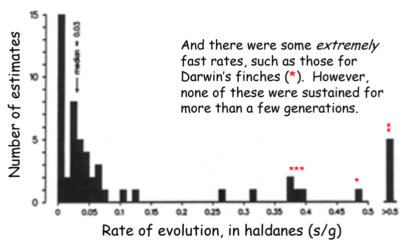
What is the "pace of modern life" for *typical* traits in *typical* species?

Hendry and Kinnison (1999) reviewed 54 rates of phenotypic evolution that had been estimated in 20 different studies of fish, birds, mammals, lizards and bugs.

They converted all of the estimated rates of phenotypic change to units of *phenotypic standard deviations per generation* (called "haldanes" because J.B.S. Haldane appears to have been the first person to suggest this standardization).

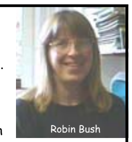
The median rate of evolution was 0.03 haldanes (3% of a s.d. per generation).

At that rate the mean would move ***3*** standard deviations in only 100 generations!



And there were some *extremely* fast rates, such as those for Darwin's finches (*). However, none of these were sustained for more than a few generations.

Some molecular phenotypes also adapt at high speeds

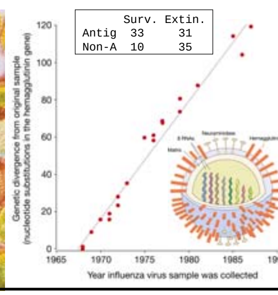


Robin Bush and her colleagues used phylogenetic analysis of frozen samples to study the evolution of the hemagglutinin protein of flu virus.

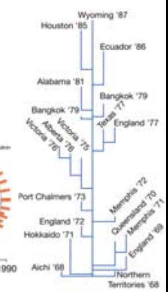
The rate of amino-acid substitution exceeds 1/yr in most lineages.

Most strains go extinct after just a few years.

The surviving lineage has *more* substitutions in *antigenic* sites (those seen by the immune system) and *fewer* in *non-antigenic* sites.



	Surv.	Extin.
Antig	33	31
Non-A	10	35



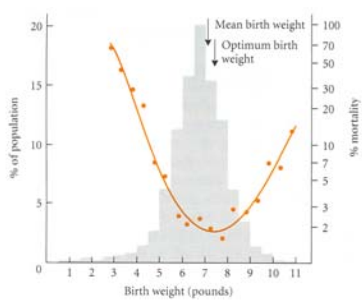
But a great deal of selection is devoted to *preventing* change

Tradeoffs often give rise to *intermediate optima*, and thus to *stabilizing selection*.

For example, modern medicine has not eliminated strong stabilizing selection on human birth weight.

Mortality rises sharply for newborns above and below the optimum weight of approximately 7.5 pounds.

What is the tradeoff that creates this optimum? What's better about being smaller? What's better about being larger?



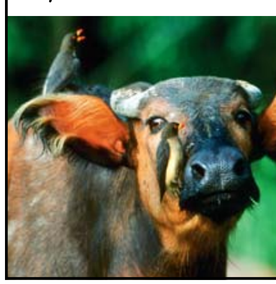
From DJ Futuyma (1998) *Evolutionary Biology 3rd edn* (Sinauer), after Cavalli-Sforza and Bodmer (1971) *The Genetics of Human Populations* (Freeman).

Is *everything* being optimized by selection? *NO!*

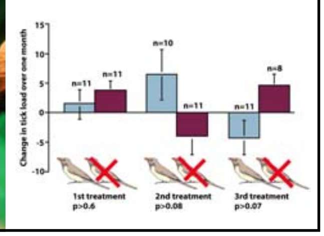
Then how can we recognize adaptations (characteristics assembled by selection)?

- Careful observation (giant velvet mites; garter-snake thermoregulation, etc.)
- Experiments (manipulating ecological circumstances or the traits themselves)
- Phylogenetic comparisons (using evolution as a "natural experiment")

Why does this forest buffalo tolerate these oxpeckers?

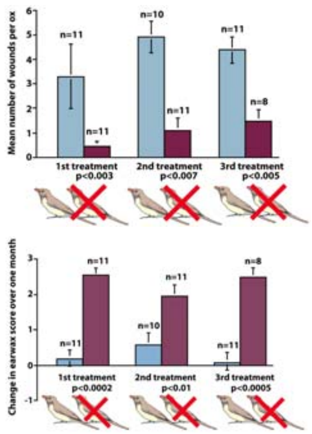


Apparently *not* to remove its ticks!

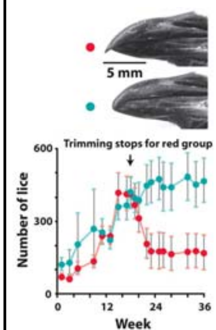


Even worse, there's a "pound of flesh" to pay for the privilege! (The birds make open wounds and feed from them!)

Could earwax-removal be the benefit?



Why the hook at the end of the beak?



Is it a feather-louse crusher?

Brett Moyer and some other students in Dale Clayton's lab trimmed the hooks off the beaks of 26 pigeons and monitored their louse loads.

Then they allowed 13 of the pigeons to re-grow their hooks, and monitored their louse loads.

Yes, it's a feather-louse crusher!

Why does this fly wave its patterned wings at jumping spiders?

H1: no reason – it's just a habit, and this fly just happens to look like a jumping spider.

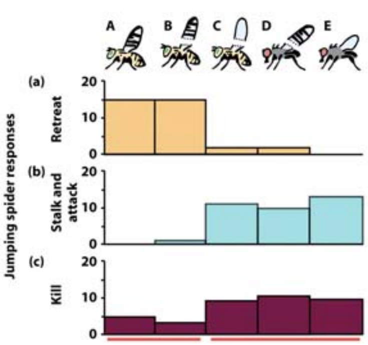
H2: mimicry deters *other* predators, who think the harmless fly *is* a jumping spider.

H3: mimicry deters *jumping spiders,* who think the fly is *another* jumping spider.

Erick Greene designed an experiment to test these three hypotheses.

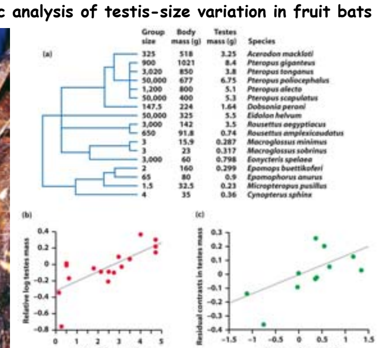
	A	B	C	D	E
Treatment	*Zonosemata* untreated	*Zonosemata* with own wings cut and reglued	*Zonosemata* with housefly wings	Housefly with *Zonosemata* wings	Housefly untreated
Purpose	Test effect of wing markings plus wing waving	Control for effects of operation	Test effect of wing waving without wing markings	Test effect of wing markings without wing waving	Test effect of no wing markings and no waving
Predictions under Hypothesis 1: No mimicry					
Jumping spider will:	Attack	Attack	Attack	Attack	Attack
Other predator will:	Attack	Attack	Attack	Attack	Attack
Predictions under Hypothesis 2: Mimicry deters other predators					
Jumping spider will:	Attack	Attack	Attack	Attack	Attack
Other predator will:	Retreat	Retreat	Attack	Attack	Attack
Predictions under Hypothesis 3: Mimicry deters jumping spiders					
Jumping spider will:	Retreat	Retreat	Attack	Attack	Attack
Other predator will:	Attack	Attack	Attack	Attack	Attack

Each of 20 spiders was presented with one fly of each kind (A-E).



Other predators (nonsalticid spiders, assassin bugs, mantises, and lizards) ate *all* of the flies efficiently and without discrimination.

Comparative phylogenetic analysis of testis-size variation in fruit bats



Yes, relative testis size increases when group size increases, and decreases when group size decreases!

Adaptation is always limited by tradeoffs and constraints.

For example, larger flowers of *Begonia involucrata* are more attractive to bees.

This is especially true for female flowers (right) which bees try to avoid because they give no reward.

Why don't female flowers evolve larger size? They would set more seeds.

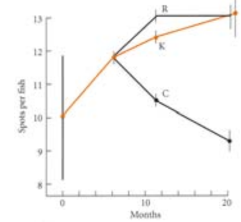
Inflorescences with *larger* flowers have *fewer* flowers, and this tradeoff appears to explain why female flowers are no larger, on average, than male flowers. (See F&H Ch. 10.6 for details.)

Female guppies like bright males, and so do predators

In Trinidad, males have fewer and duller spots in streams with a strong predator, *Crenicichla* [C], than in streams with a weak predator, *Rivulus* [R].

To test the hypothesis that males face a tradeoff between mating success and predator avoidance, John Endler set up artificial stream populations with guppies from a *Crenicichla* stream in Trinidad.

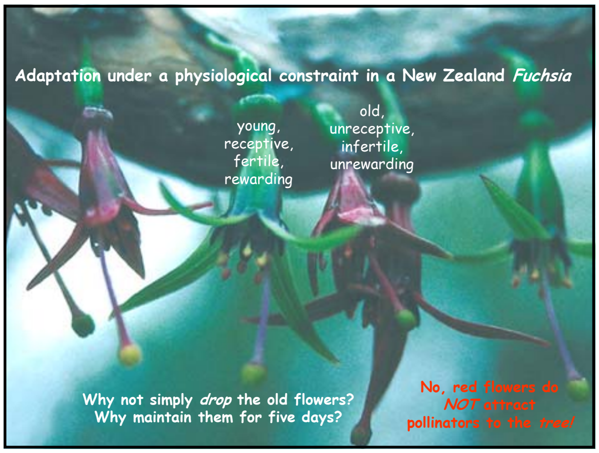
Then after six months he added either *Crenicichla*, *Rivulus*, or no predator at all [K], and waited…



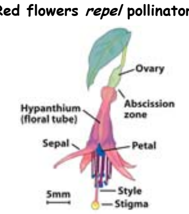
John Endler

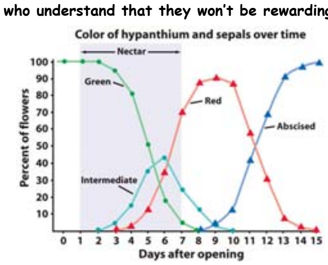
Classic experiment, done right here!

male guppy, *Poecilia reticulata*



Red flowers *repel* pollinators, who understand that they won't be rewarding.





But some pollen tubes need four days to reach the ovary, so dropping the flower during pollen-tube growth would reduce seed set.

Curt Lively & Lynda Delph

Table 10.2 Pollen tube growth in *Fuchsia excorticata*

Days since pollination	1	2	3	4
Percentage of 10 flowers with pollen tubes in ovary	0	20%	100%	100%

Source: After Delph and Lively (1989).

Environmental variation is probably the source of many tradeoffs

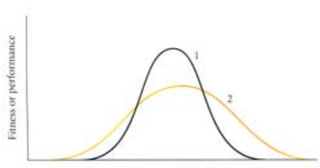
Being optimized for a particular environmental condition makes a trait (like "1" in the figure on the right) less fit in other conditions.

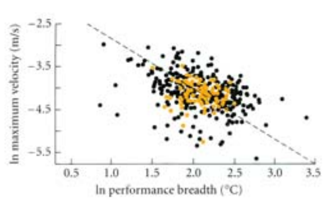
But what about being *flexible* (adjustable for different conditions)?

Will a more flexible "generalist" phenotype (2) usually have a lower *maximum* fitness than a less flexible specialist phenotype?

The lower figure shows data on maximum running speed *versus* the width of the performance curve for speed as a function of temperature, for a parasitoid wasp (*Aphidius ervi*). The black points are individuals, and the colored points are family means.

The negative relationship implies a cost of broad thermal tolerance, as represented schematically in the upper figure.





Summary

Adaptive evolution appears to be ongoing in most species at most times.

Stabilizing selection (maintaining adaptation) is ubiquitous.

But organisms have many features that lack adaptive functions, and the functions of some traits can be hard to determine.

Organisms are far from perfect! The reasons include:

Tradeoffs (the "no free lunch" principle). Guppy color spots, etc., etc.

Pleiotropy ("you can't do just one thing"). Flower abscission in *Fuchsia*.

Opportunity ("you can't get there from here"). Selection acts only on *available* genetic variation. We're stuck with four limbs.

Genetic load ("most changes are for the worse"). Mutations happen, and locally maladapted alleles migrate in from elsewhere. This is one reason why there will always be stabilizing selection.

Evolutionary lag ("always fighting the last war"). Populations are better adapted to some *past* environments than to present ones, because evolution takes time. Just ask Darwin's finches…