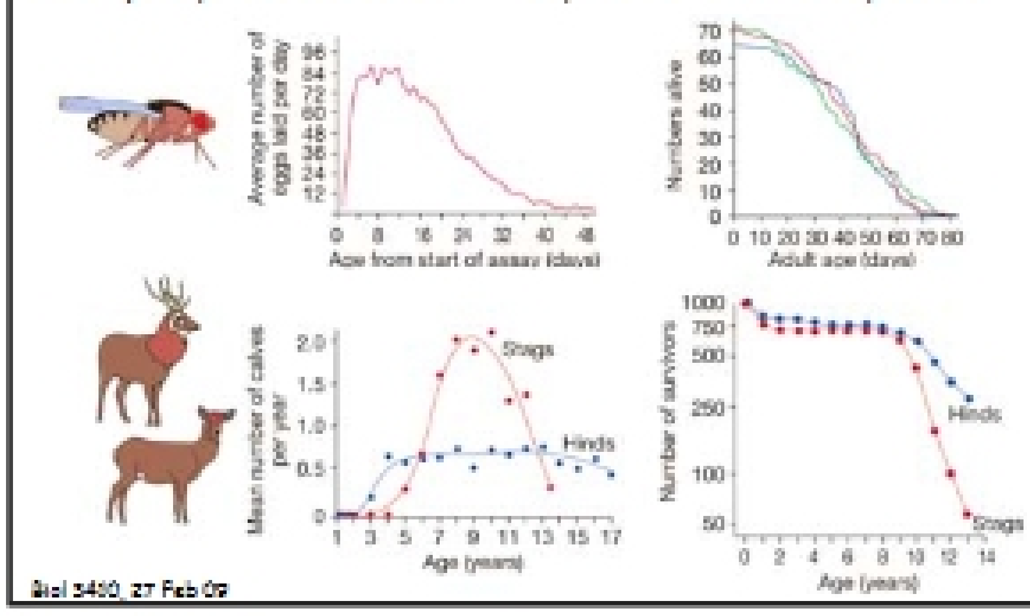
Life-history evolution: why life's a grind and then we die

Why is death life's only certainty (other than taxes, and declining vigor)?

Why do the sexes often senesce at different rates?

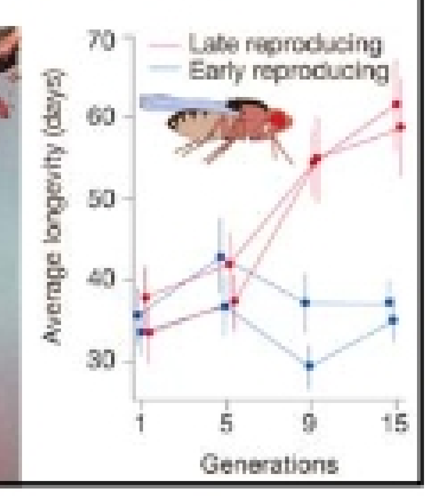
And why do species differ so much in life spans and schedules of reproduction?



The *rate-of-living theory* can't explain it!

The most popular theory is that organisms simply *wear out*, through inability to repair all oxidative damage, mutations, and the like.

This theory predicts that the rate of aging should be directly tied to metabolic rate, and that species should not be able to evolve longer life spans without reducing their metabolic rate.



The *evolutionary theory of aging*: selection weakens as life advances

In the early 1950s, Peter Medawar pointed out that selection against deleterious mutations with effects that appear only *late* in life will be much weaker than selection against equivalent mutations with effects *early* in life, if there is inescapable *extrinsic* mortality.

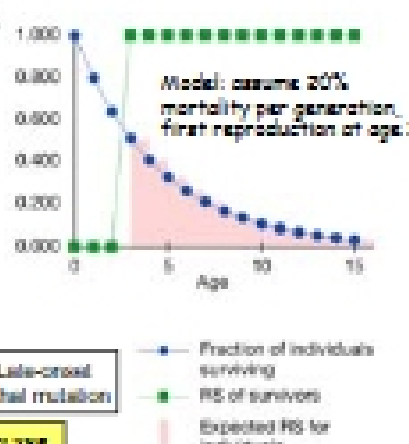
Late-effect mutations will therefore accumulate at much higher rates than early-effect mutations, causing senescence.

Sir Peter Medawar

Age	Fraction of individuals surviving	RS of survivors	Expected RS for individuals
0	1.000	0	0.000
1	0.800	0	0.000
2	0.640	0	0.000
3	0.512	1	0.512
4	0.410	1	0.410
5	0.328	1	0.328
6	0.262	1	0.262
7	0.210	1	0.210
8	0.168	1	0.168
9	0.134	1	0.134
10	0.107	1	0.107
11	0.086	1	0.086
12	0.069	1	0.069
13	0.055	1	0.055
14	0.044	1	0.044
15	~~0.035~~	~~1~~	~~0.035~~

Late-onset lethal mutation

Expected lifetime RS: ~~2.419~~ 2.385



And *early* reproduction is worth much *more* than late reproduction

In the late 1950s, George Williams pointed out that mutations with harmful (even lethal) effects *late* in life could be positively favored by selection if they also increased *early* reproduction.

Such "pleiotropic" tradeoffs between early and late fitness can explain the *adaptive* evolution of *shortened* lifespans (that is, mortality).

Professor Emeritus George C Williams (Ecology & Evolution, SUNY Stony Brook)

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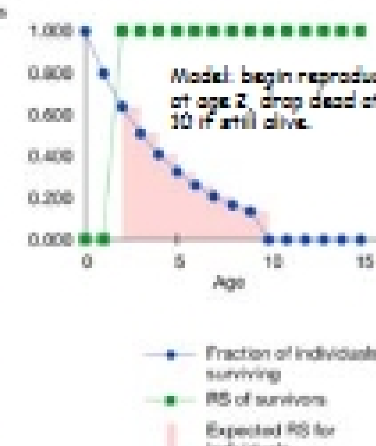
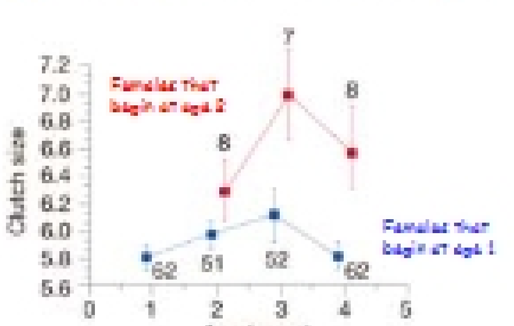
13	0.000	1	0.000
14	0.000	1	0.000
15	0.000	1	0.000

Expected lifetime RS: 2.663



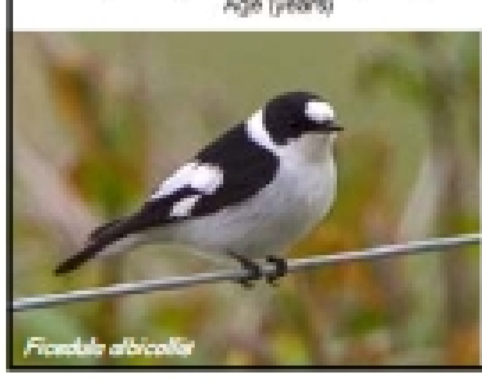
If the evolutionary theory is correct, life histories are shaped by (1) rates of extrinsic mortality, and (2) the costs of reproduction



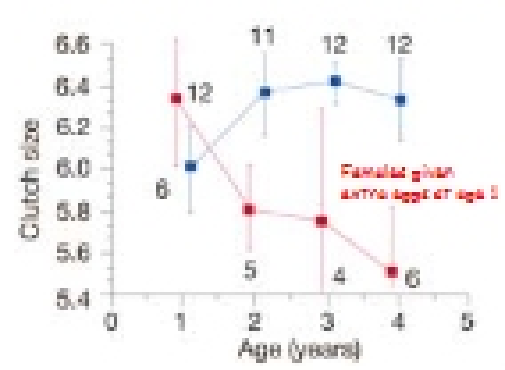
Extrinsic mortality rates vary greatly (*e.g.*, rodents > bats), and so do rates of senescence (*e.g.*, rodents > bats).

Reproduction (especially early reproduction) is costly, as shown by these data for collared flycatchers (*Ficedula albicollis*).

Even so, females that begin at age 1 have higher lifetime fitness (1.24 offspring) than those that begin at age 2 (0.90 offspring). (Gustafsson and Pärt, *Nature* 347, 279-281, 1990)

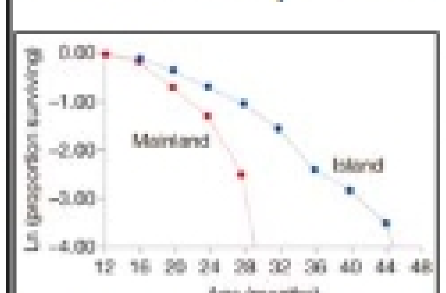


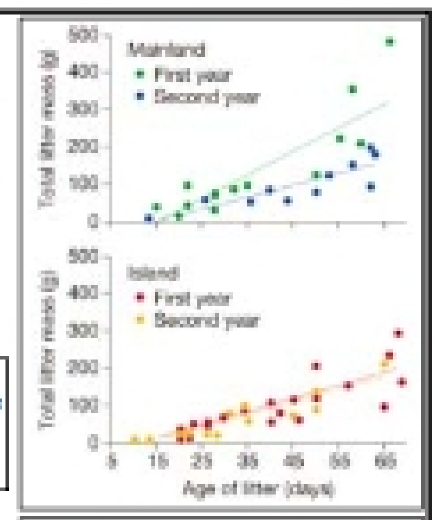
Ficedula albicollis



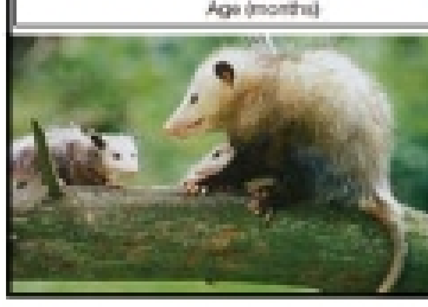
Rates of senescence should evolve *downward* when extrinsic mortality is lowered

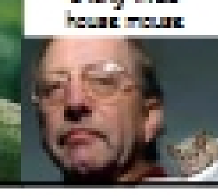
Virginia opossums on predator-free Sapelo Island age and reproduce more slowly than those on the neighboring South Carolina mainland, where many individuals are killed by bobcats and other predators.



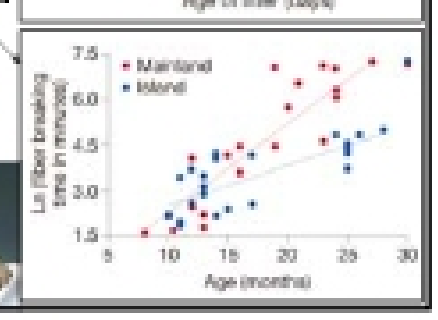


Collagen cross-linking in tendons even goes more slowly in the island 'possums!





Steven Austad with his friend, a long-lived house mouse



Offspring size and number: a fundamental tradeoff

Selection favors the fittest phenotype, right?

Yes, by definition.

When it comes to offspring, more is better, right?

Yes, other things being equal.

So what's not equal?

Resources. Like food, for example.

Oh. So the kids each get less in big families?

Yes, something like that.

OK, so what's the fittest family size?

The one that maximizes the parents' fitness.

That would be the *sum* of the kids' fitnesses, right?

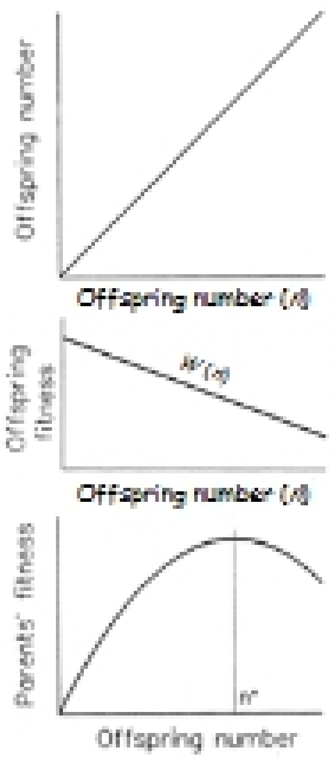
Right!

*n*W(n)*?

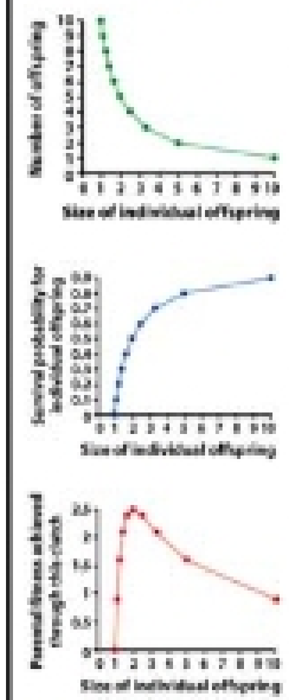
Right!

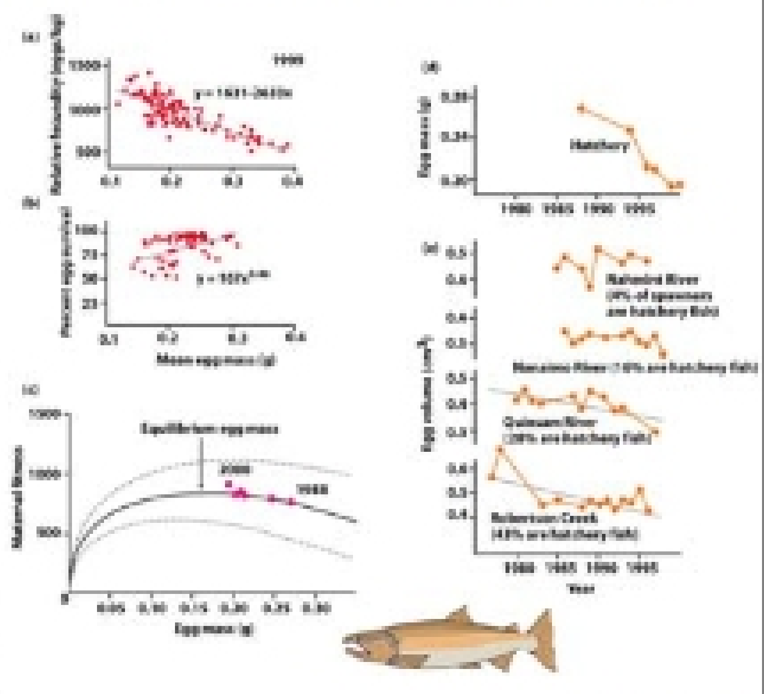
So we just take the derivative with respect to *n* (the number of offspring), set it equal to zero, and solve?

Right! Do it!



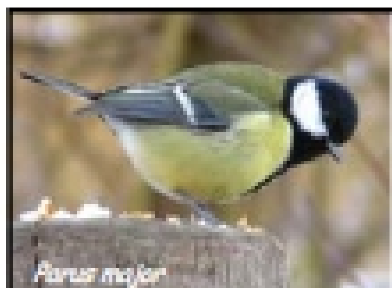
The theory: The theory in action: evolution of salmon egg size





Smith & Fretwell (1974)

Heath et al. (2003)

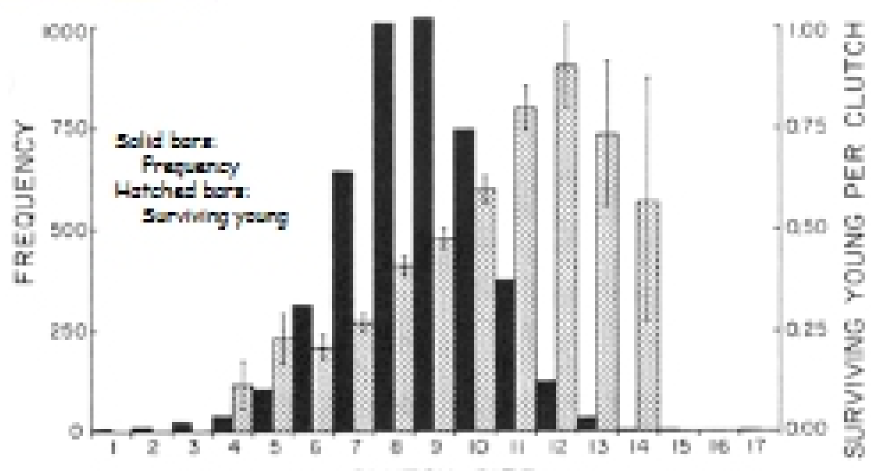


Birds should lay the number of eggs that maximizes their number of surviving young.

The great tits (*Parus major*) in Wytham Wood have been followed for decades by David Lack and his students.

The most frequent clutches are much *smaller* than the most productive clutches.

What's going on? Don't these birds care about fitness?



To address this question, Lack and his students manipulated clutch sizes.

They added 1-4 eggs to some nests and removed 1-7 eggs from others, then followed the fates of the parents and chicks.

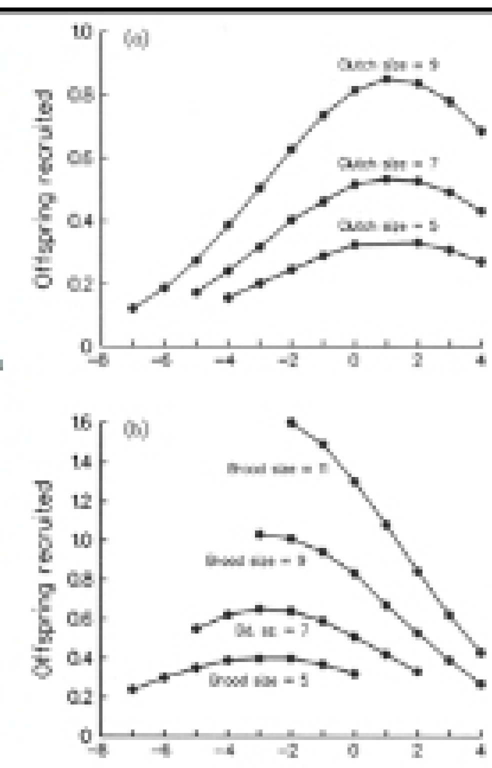
Adding more than one or two eggs almost always resulted in a *lower* reproductive success for the parents.

This result suggests that parents know what they're doing when they decide to lay a clutch of a certain size!

Parents differ in ability to provide for offspring, and they adjust their clutch sizes to their current conditions.

Typical (9-egg) parents are maximizing their expected reproductive success, *under the circumstances*, as are *all* parents.

We infer that the evolved "function" of a clutch-size "decision" or "strategy" is to help the parents fledge as many healthy chicks as they can, given their current condition.



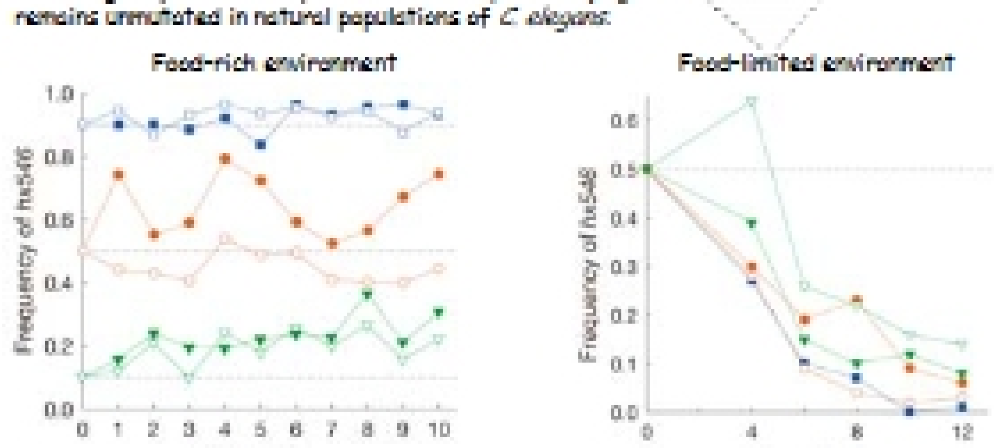
A "longevity gene" in *Caenorhabditis elegans*?

The *AGE-1* protein is a kinase (protein phosphorylating enzyme) required for the regulation of metabolism, stress resistance, embryonic development, and life span.

Mutations in the *age-1* gene increase lifespan by up to 80%.

One of these mutations (*hx546*) is selectively neutral in a food-rich environment but *deleterious* under food limitation.

Thus longevity comes at a price, and this explains why *age-1* remains unmutated in natural populations of *C. elegans*.

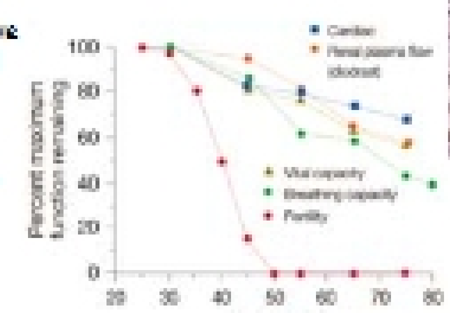


Why do human females live long after last reproduction?

Few other animals do this, and it is *not expected*. (Why?)

Kristen Hawkes and her colleagues have proposed that non-reproductive grandmothers help their daughters reproduce by helping to feed (and otherwise care for) the daughter's older children.

In support of this hypothesis, they have gathered data showing that older women are extremely productive as foragers in modern hunter-gatherer societies.



Distinguished Professor Kristen Hawkes (Anthropology, Univ. of Utah)

A 65-year-old Hadza woman gathers tubers