Intuitive and not-so-intuitive outcomes in life history evolution

Matthias Galipaud

Lotte de Vries

Hanna Kokko, University of Mainz, Germany

Let's define the question

credit: Randall Munroe (xkcd.com)

For the purpose of this talk, I'll redefine the product:

it'll only give you protection from senescence,

but not e.g. from being run over by a bus

extrinsic mortality

What sort of life expectancy do they give you?

Fact of the day: We die at a rate of about 1 micromort per day (non-natural causes, suicide excluded)

→ With these shoes you'd live about 1 million days (approx. 2700 years)

If you lived in a very dangerous society,

would that make you value these shoes less?

George
Williams
thought
it should.

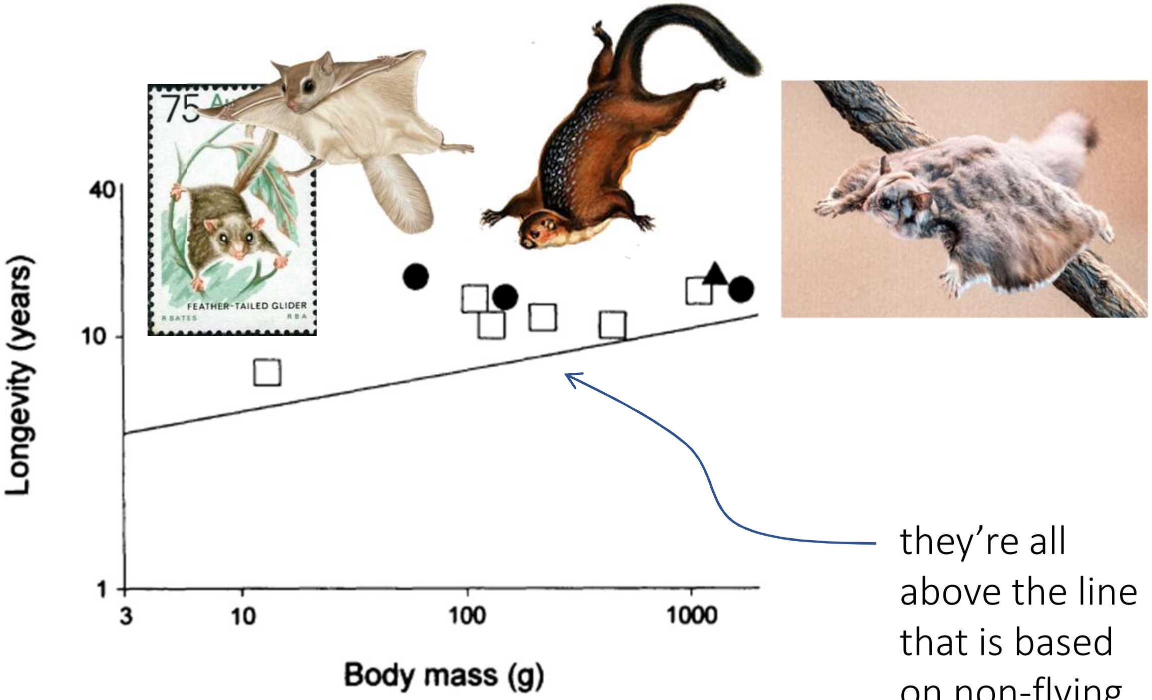
If unavoidable (‘extrinsic’) mortality is high, building a robust body is pointless and thus not favoured by selection

‘Williams hypothesis’

Does lower extrinsic mortality lead to slower senescence?

FLY NOW, DIE LATER: LIFE-HISTORY CORRELATES OF GLIDING AND FLYING IN MAMMALS

DONNA J. HOLMES AND STEVEN N. AUSTAD



they're all above the line that is based on non-flying mammals

Bats are also very long-lived for their size (Wilkinson & Adams 2019)

Wisdom The Albatross, Now 70, Hatches Yet Another Chick

March 5, 2021 · 11:08 AM ET

BILL CHAPPELL

Wisdom, a mōlī or Laysan albatross, and the world's oldest known banded wild bird, hatched a new chick at Midway

Wisdom, the World's Oldest Known Wild Bird, Returns to Midway Atoll

Dec 9, 2022

'Wisdom' already had adult plumage when banded in 1956

…a year before Williams proposed his theories about senescence

Yet modellers can't even agree on whether this prediction is valid!

Reports of the Death of Extrinsic Mortality Moulding Senescence Have Been Greatly Exaggerated

Jack da Silva[1]

Received: 22 June 2017 / Accepted: 15 February 2018

Evolutionary Ecology of Senescence and a Reassessment of Williams' 'Extrinsic Mortality' Hypothesis

Jacob Moorad,[1] Daniel Promislow,[2,@] and Jonathan Silvertown [1,*,@]

The claim that the classic theory does not predict an increase in the rate of senescence with an increase in extrinsic mortality is strictly incorrect. With the **realistic assumption of a constant population size on an evolutionary time scale,** the intuition of G. C. Williams (1957) is correct (Hamilton 1966) and **empiricists have not been misguided** in using this strong prediction to test the theory.

[…] da Silva [30] has argued that *r* = 0 is of special relevance in this context because populations over time must have some long-term average growth rate that approximates this value.

Fortunately, models that explicitly consider how age-independent mortality affects selection in fluctuating age-structured populations with arbitrary growth rates [6,31] find **no effects on selection.**

The use of 'arbitrary' sounds like this is a more general model.
But there's an assumption in there too – the age-independence one.

Why would extrinsic mortality *not* impact selection to delay senescence?

intuition:
selection to delay senescence is

	Extrinsic mortality	Survival	
	80% between each breeding attempt*)	20%	weak(er)
	40%	60%	strong(er)

*) including from birth to 1st breeding

To make this a senescence model, we will additionally assume there's an intrinsic decay process

if it's rapid, then you can only maximally breed once
if it's slow, then you can breed twice

because your body is more robustly built

Huh? No-brainer!
Having a robust body
(in this example)
is always selected for.

Yes ...but is the bat
selected to do it
more strongly?

Number of times a newborn mouse or a bat will breed if…

	it dies after breeding once	it dies after breeding twice
	0.2	$0.2 + 0.2 \times 0.2 = 0.24$
	0.6	$0.6 + 0.6 \times 0.6 = 0.96$

By how much did expected lifetime reproductive success increase?
0.24/0.2 = 1.2, i.e. 20% improvement
0.96/0.6 = 1.6, i.e. 60% improvement

Case closed – bat is more strongly selected to try to reap the benefits of long life?
No, no, no, no, no.

Because… the bat will also (all else being equal) have a threefold pop. growth rate *)
After all, it survives 3 times as well.

This 3-foldness may be intuitively obvious, but if not: here's the Euler-Lotka equation

$$\sum_{a=1}^{\omega} \lambda^{-a} l(a) b(a) = 1$$

growth

(mean) reproductive output of these survivors

proportion of individuals surviving to age *a*

F = fecundity

For the mouse, we need to solve

$$\frac{1}{\lambda}\frac{1}{5}F + \frac{1}{\lambda^2}\left(\frac{1}{5}\right)^2 F = 1$$

For the bat, we need to solve

$$\frac{1}{\lambda}\frac{3}{5}F + \frac{1}{\lambda^2}\left(\frac{3}{5}\right)^2 F = 1$$

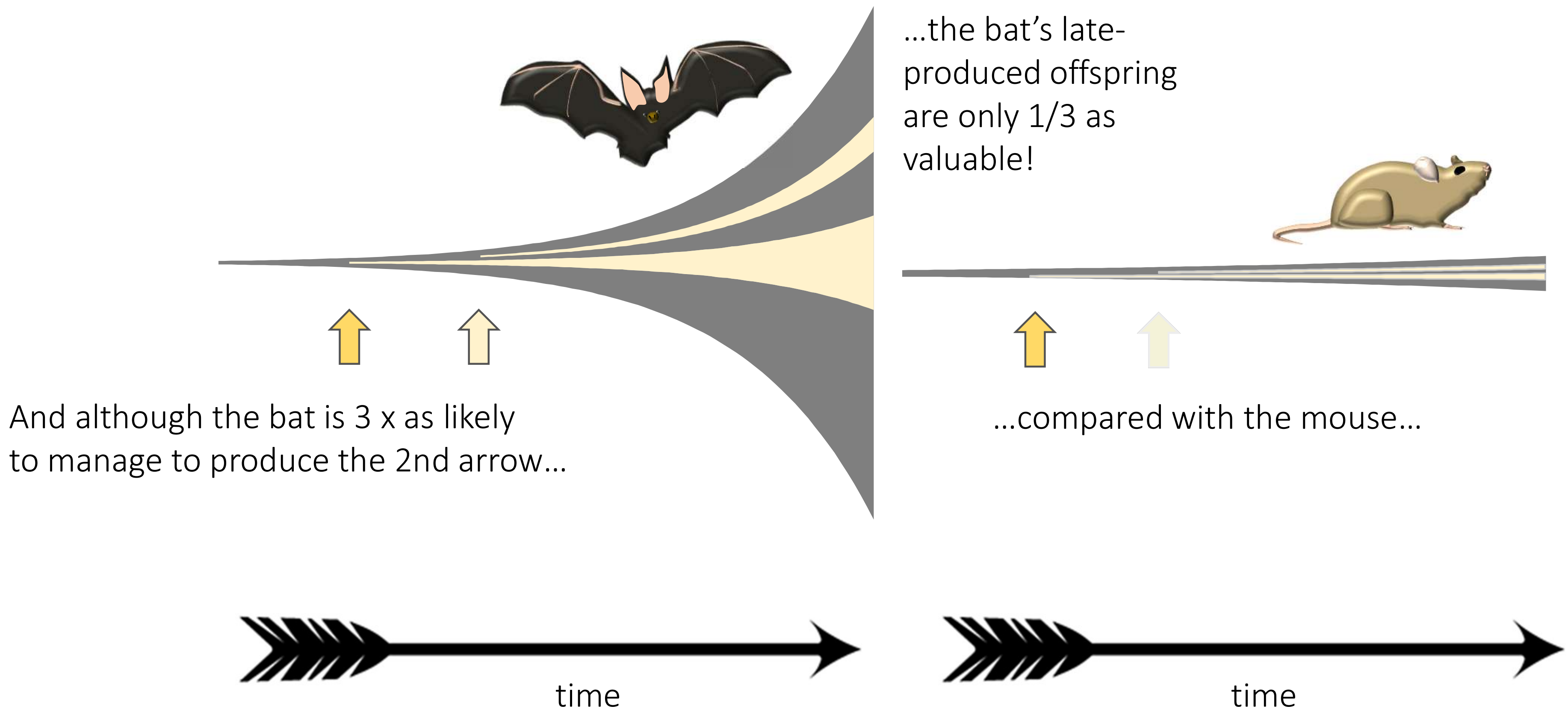
$$\lambda = \frac{1}{10}\left(F + \sqrt{F^2 + 4F}\right)$$

$$\lambda = \frac{3}{10}\left(F + \sqrt{F^2 + 4F}\right)$$

*) Really? (Wait.)

If high survival is allowed to translate into high population growth ‘just like that’

then the bat population will expand much quicker than the mouse population,



The trumpet shape

(a.k.a. exponential growth of the population)

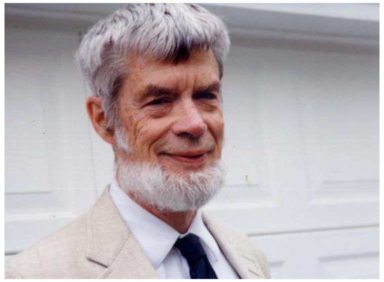
cancels out all benefits that we use to argue that bats should delay senescence more than mice

But can the trumpet expand forever?

Fact is, we don't observe Darwinian demons around us.

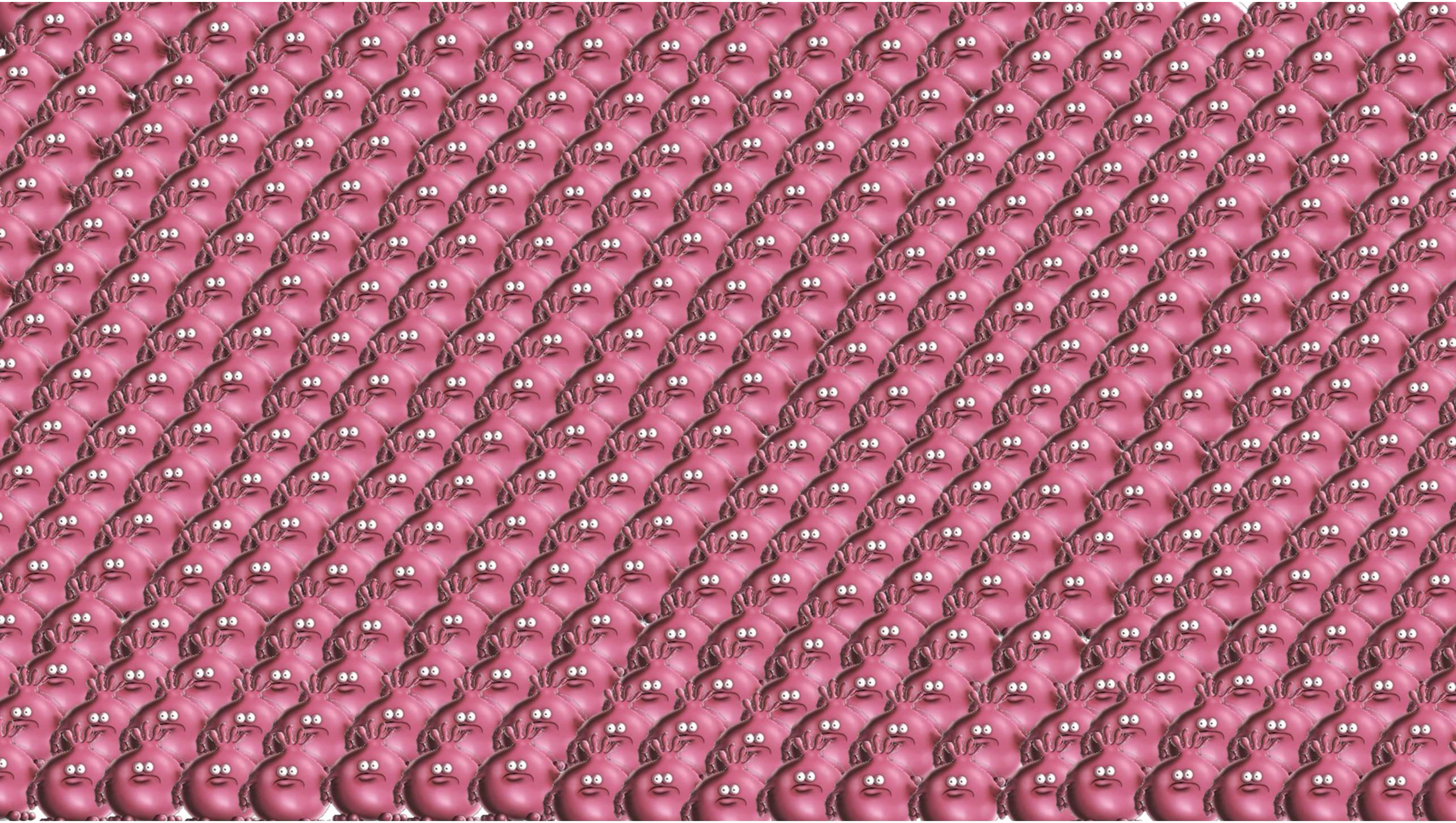
Observe… what?

George Williams' brainchild, 1966



Darwinian demon:

an organism that matures immediately after birth, survives forever, and has infinite fecundity.



Evolution is very much about managing limited resources. Let's think about whales

One sperm whale takes approx. 20 cubic metres of volume (females are a bit smaller, males are substantially bigger, so this is a conservative estimate of the average)

Total ocean area = 361 900 000 km^2

Average ocean depth = 3688 m

How many cubic metres in all oceans?

1.3347×10^{18} m^3

We would need 1.3347×10^{18} / 20 sperm whales to fill all the oceans

(so that no water is left between them)

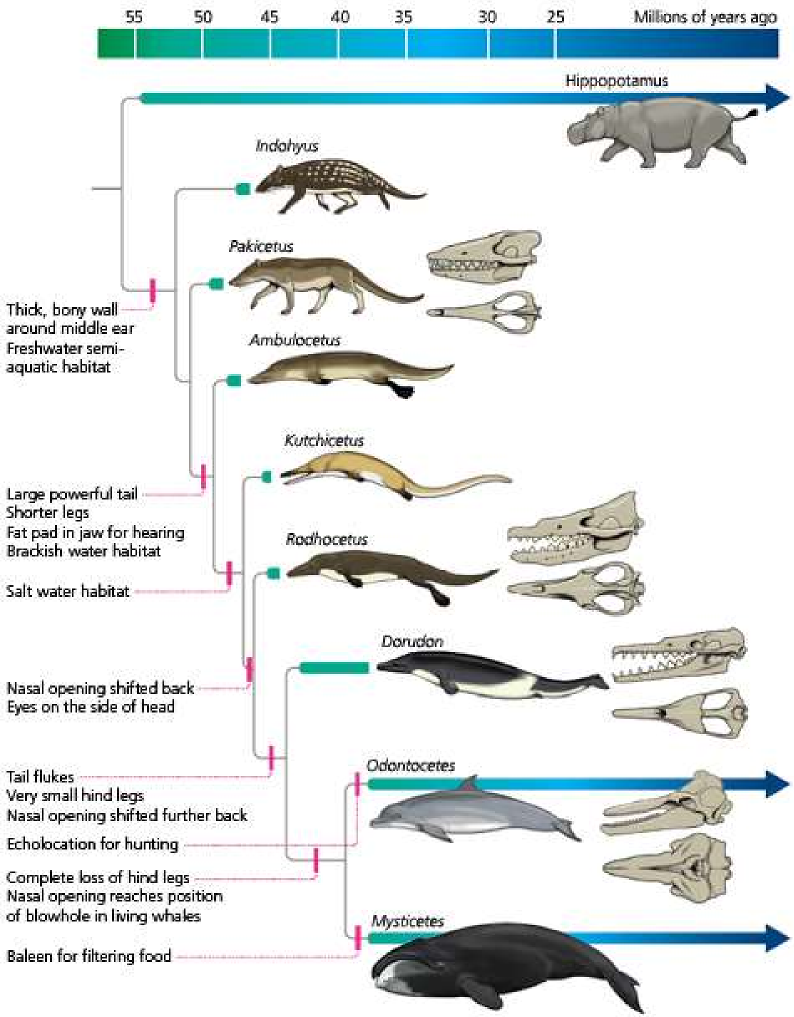
That is approx 6.7×10^{16} sperm whales

Let's start from the current population size, let's guess it to be 300 000, and 3% population growth (realistic for big things like humans and whales)

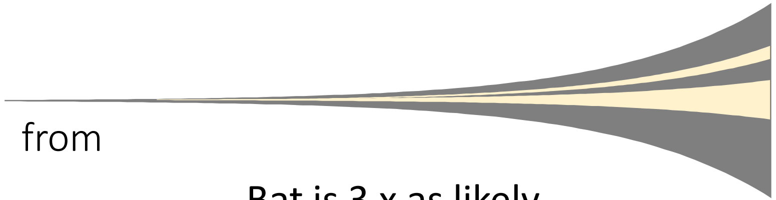
Guess! How many years would it take for all ocean water have turned into whale biomass?

Answer: 800 years.

In reality, whale-like organisms have existed for a *lot* longer than 800 years and they obviously haven't replaced the seawater.



We expect long-term processes to be near an ecological equilibrium, where $r \approx 0$

from  to 

Here the bat appears to be safe from the cancelling effect! BUT…

Bat is 3 x as likely
to create an extra offspring
but it's only 1/3 worth it

Bat is 3 x as likely
to create an extra offspring
and it's 100% worth it

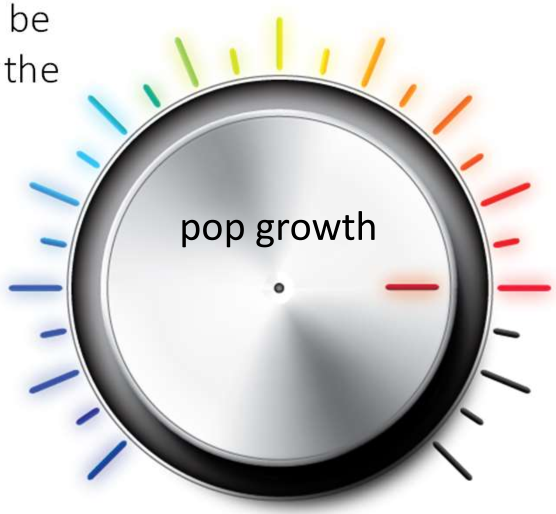
The key point is:

Reducing growth rates cannot be done just like that, by 'dialling the growth rate parameter down'

- without changing something in the participants' lives.

Some existing individuals must die,

or reproduce less well.



Is it OK to assume that the bat kept its survival intact now that its population cannot grow?

Investigating this topic also gives us the opportunity to remember that fecundities differ between bats & mice!

Model: We contrast 2 life histories:

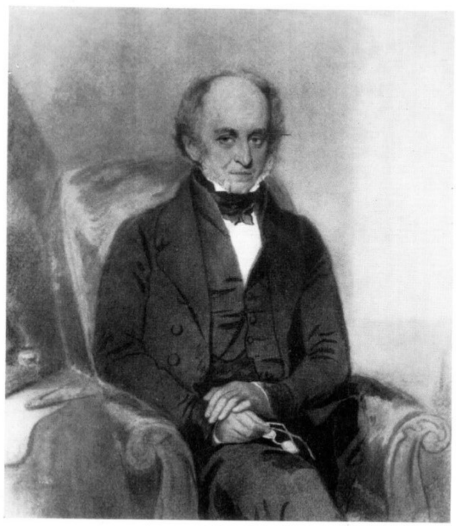
FAST and SLOW

SLOW genotypes have a more sluggish reproductive rate

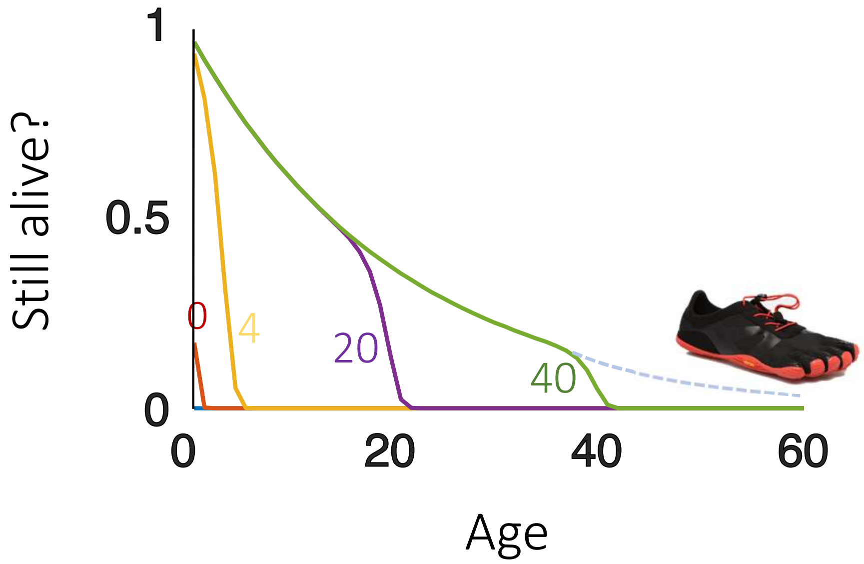
but avoid senescence.

The FAST one senesces according to Gompertz-Makeham mortalities

but produces more offspring per attempt.



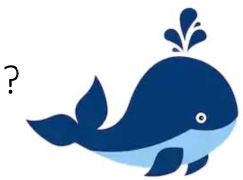
BENJAMIN GOMPERTZ, 1779–1865



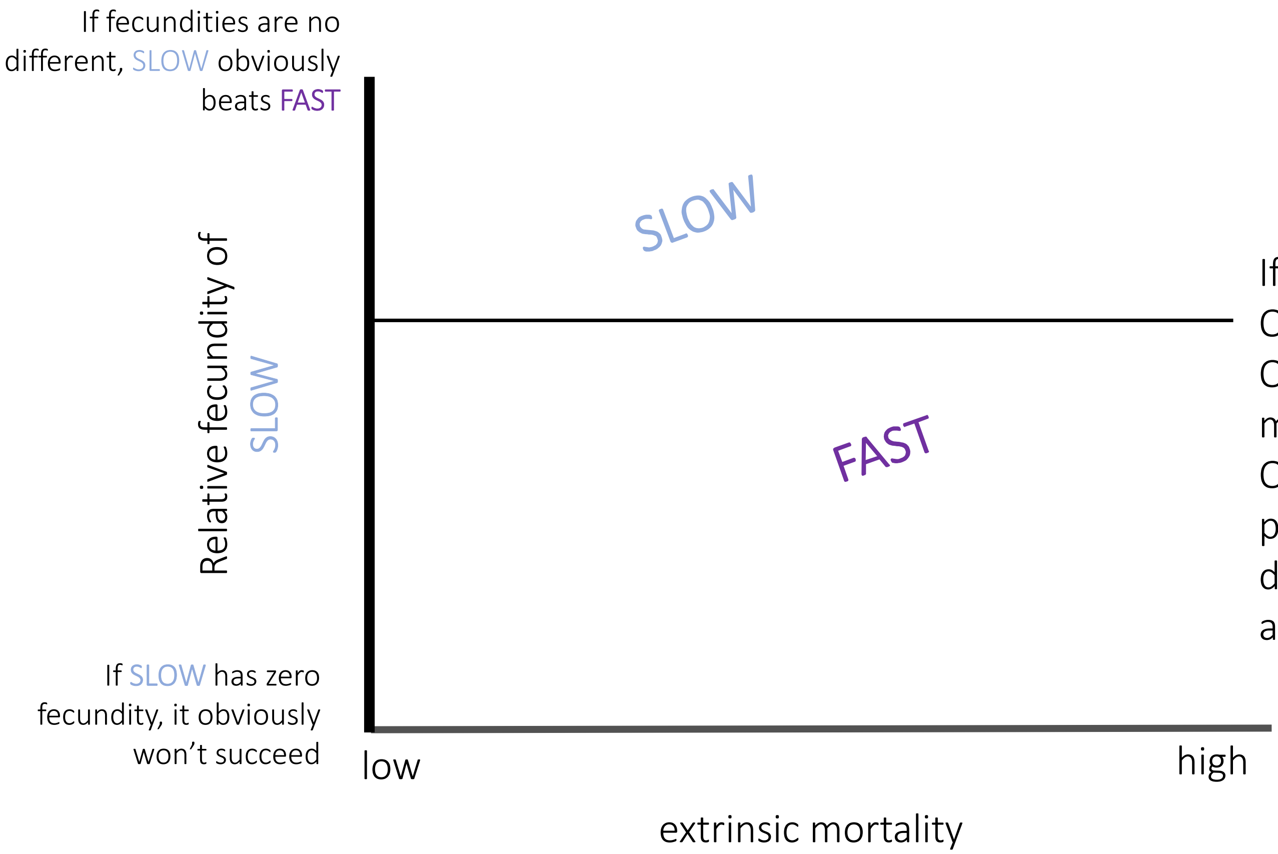
Q1: how big should the fecundity difference be for FAST to outcompete SLOW?

Q2: does this threshold depend on extrinsic mortality?

Q3: does the answer to Q2 depend on population regulation?



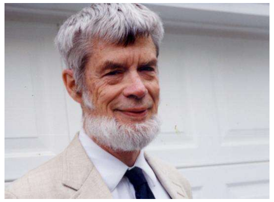
The logic of the pictures is like this:

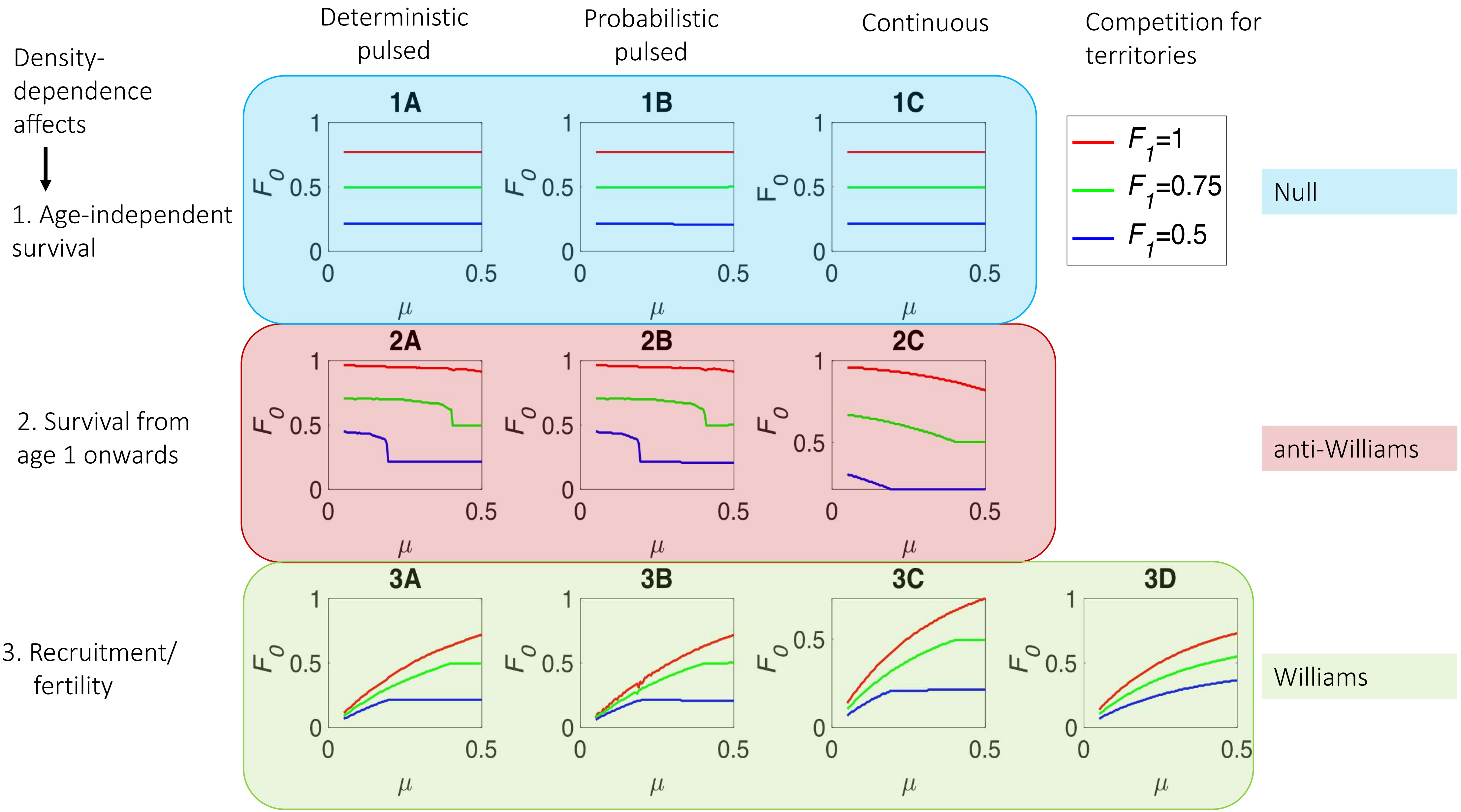


If we find a flat line…
Q1. The required ratio is here
Q2. no effect of extrinsic mortality
Q3. Let's see if flatness prevails (or not) across different ways to regulate a population

The logic of the pictures is like this:

Is this possible? “Anti-Williams”





Deterministic pulsed
Probabilistic pulsed
Continuous
Competition for territories
Density-dependence affects
1. Age-independent survival
2. Survival from age 1 onwards
3. Recruitment/ fertility
1A
1B
1C
2A
2B
2C
3A
3B
3C
3D
F0
μ
F1=1
F1=0.75
F1=0.5
Null
anti-Williams
Williams

"There is rather broad empirical support for Williams-type patterns across species (e.g. Ricklefs, 2008), which may be seen as indirect evidence that population regulation often operates via this mode."

Peer Community Journal

Section: Evolutionary Biology

RESEARCH ARTICLE

Published
2023-03-24

Cite as
Charlotte de Vries, Matthias Galipaud and Hanna Kokko (2023) *Extrinsic mortality and senescence: a guide for the perplexed* , Peer Community Journal, 3: e29.

Correspondence
c.devries@uva.nl

Extrinsic mortality and senescence: a guide for the perplexed

Charlotte de Vries[1,2,3], Matthias Galipaud[3,4], and Hanna Kokko[3,5,6,7]

Volume **3** (2023), article e29

https://doi.org/10.24072/pcjournal.253

Peer Community Journal

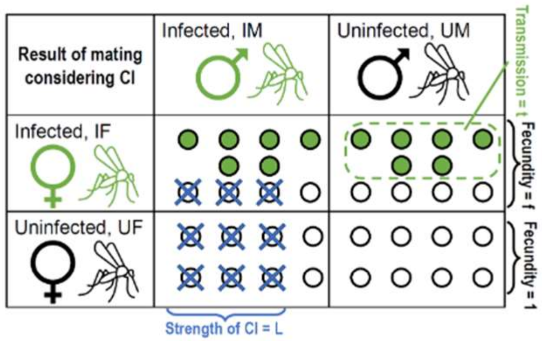
Search articles, authors... | Search | Browse by volumes | Browse by section

« | Browse issues | Volume 2 (2022) | article no. e76 | »

Ecology

Positive fitness effects help explain the broad range of *Wolbachia* prevalences in natural populations

Karisto, Petteri[1, 2] ; Duplouy, Anne[3] ; de Vries, Charlotte[1, 4] ; Kokko, Hanna[1, 5, 6]



10.24072/pcjournal.202 - Peer Community Journal, Volume 2 (2022), article no. e76.

Get full text PDF | Peer reviewed and recommended by PCI

Exzellenz verbindet – be part of a worldwide network

Alexander von HUMBOLDT STIFTUNG

Matthias Galipaud

Lotte de Vries

FNSNF

FONDS NATIONAL SUISSE
SCHWEIZERISCHER NATIONALFONDS
FONDO NAZIONALE SVIZZERO
SWISS NATIONAL SCIENCE FOUNDATION