Life histories, fitness, and demographic heterogeneity

EEE330 · Lecture 2

Why do organisms live so differently?



Individuals are not equivalent

From Lecture 1: *Why do individuals differ? Does age or stage structure matter?*

Which panthers can survive, reproduce, or change state next year?



Kitten

survive, grow



Subadult

survive, mature



Breeding adult

survive, reproduce



Older adult

survive, reproduce?

One population total conceals different demographic futures.

Contrasting lives

Sketch how survival and reproduction change with age in each.



Bank vole

Early maturity
Several litters
Short life



Asian elephant

Late maturity
One calf at long intervals
Long life



Sockeye salmon

Delayed maturity
One spawning
Death after spawning

Answer ›

Two genotypes, two schedules

Two genotypes. Everyone survives to age 3, then dies. Both produce 2 offspring in a lifetime.

Age	1	2	3
Genotype A	1	1	0
Genotype B	0	0	2

Start each with one newborn. Who has more living descendants after 12 years?

Answer ›

Four summaries of fitness

Fill in the table: which measures can tell A from B?

	LRS	R_0	T	λ
A	?	?	?	?
B	?	?	?	?

$$\lambda \approx R_0^{1/T}$$

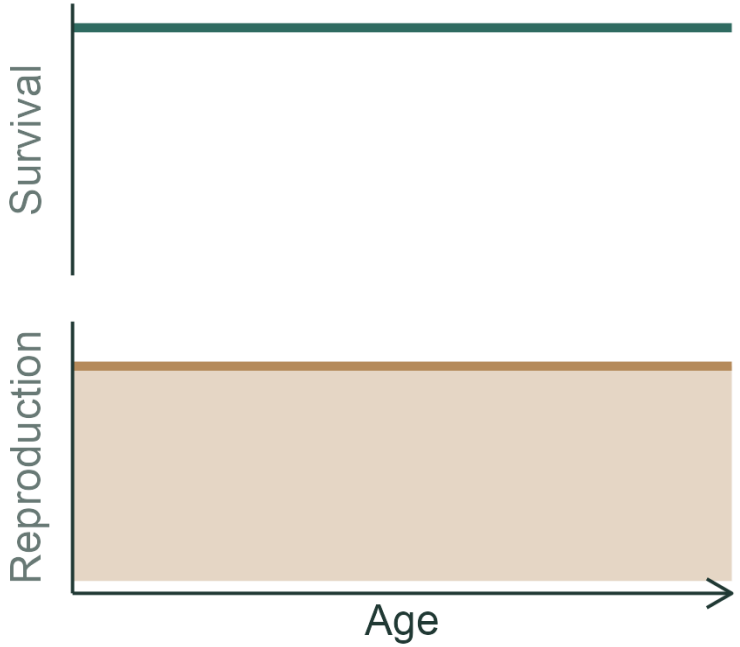
LRS: lifetime reproductive success · R_0: expected offspring per generation · T: mean age of reproduction · λ: growth factor per year

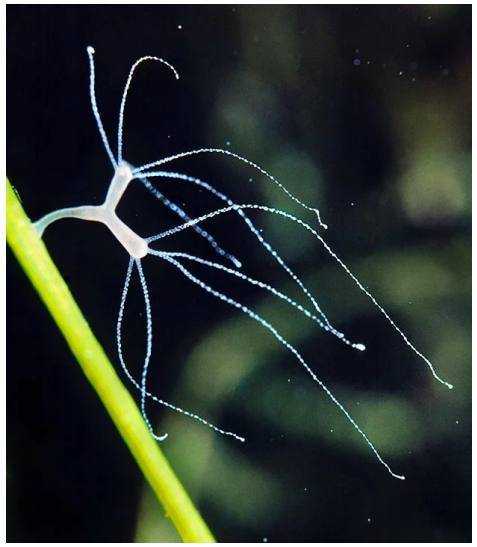
Answer ›

The Darwinian demon



Mythological hydra





Real Hydra

Survive forever

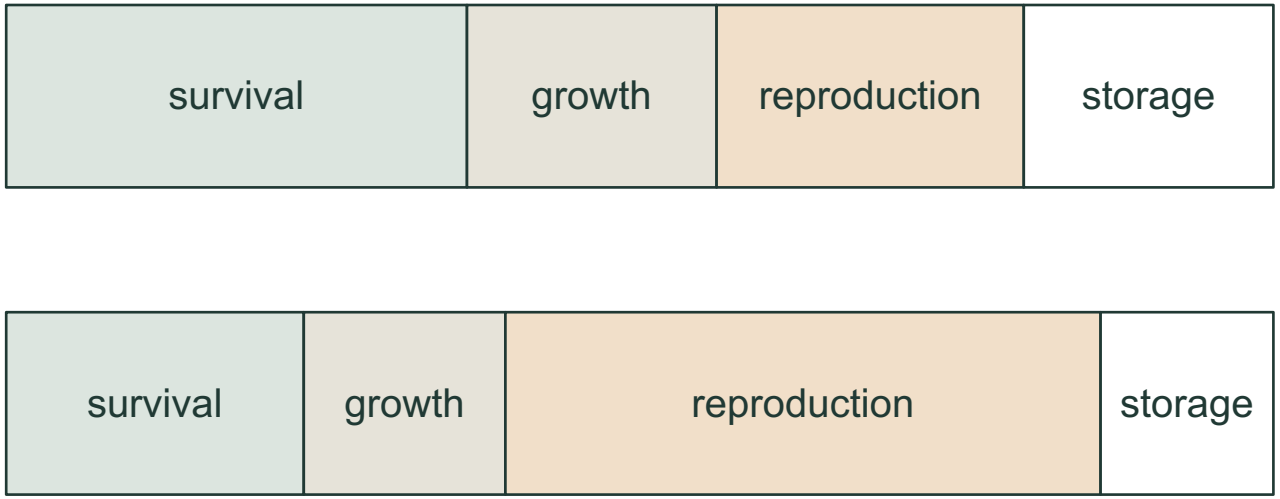
Mature immediately · Reproduce without limit

Why has natural selection not produced this organism?

Finite resources, physiology, ecological risk — and trade-offs

Allocation creates trade-offs

The same acquired resources, allocated differently



More to reproduction leaves less for survival and storage.

Trade-off: a change that benefits one fitness component costs another.

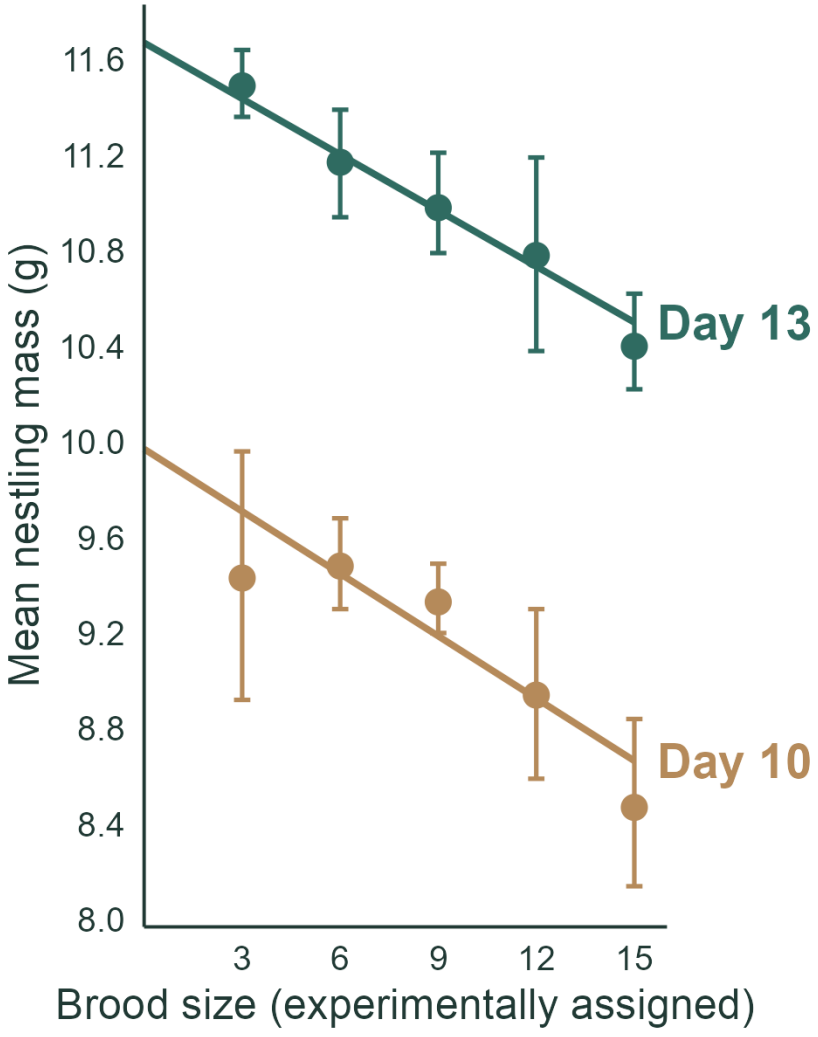
reproduction now vs survival

reproduction now vs reproduction later

offspring number vs size or condition

reproduction vs growth

More blue-tit chicks, lighter nestlings



1979 broods; means ± SE
Redrawn from Nur 1984, J. Anim. Ecol., Fig. 2

Breeding pairs were given experimentally enlarged or reduced broods (3–15 young).

What do the parents gain?
What does each chick lose?

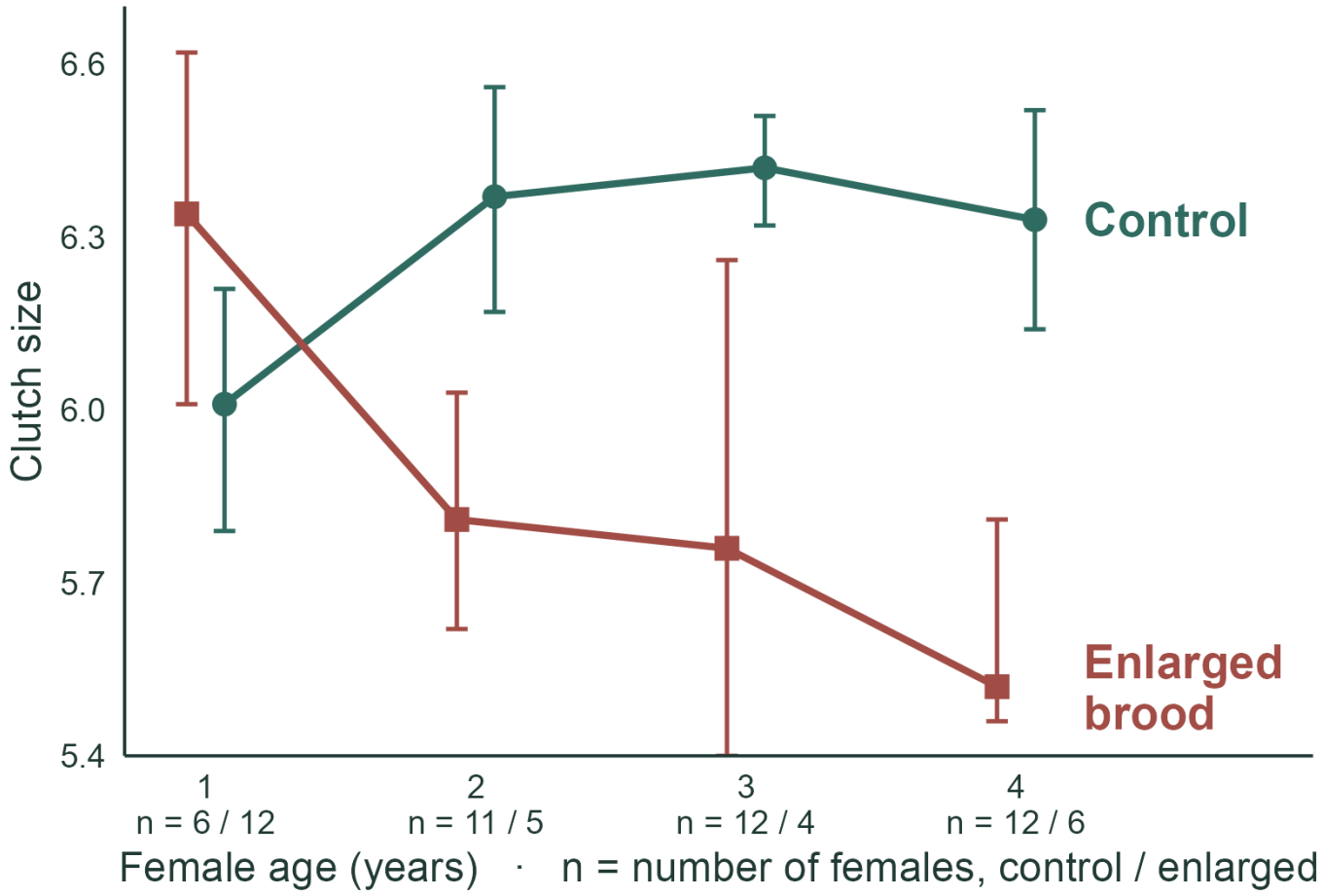


Nestling mass is not a complete measure of fitness.

Trade-off: offspring number vs condition

Reproducing now can cost reproduction later

Collared flycatcher females given an enlarged brood in their first year laid smaller clutches in later years than controls.



Redrawn from Gustafsson & Pärt 1990, Nature

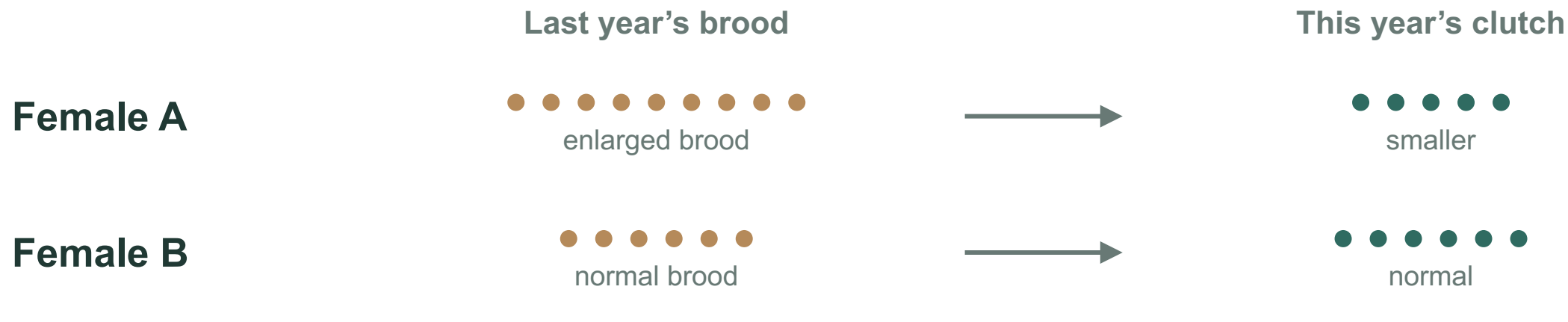


What was gained now, and what was lost later?

Trade-off: reproduction now vs reproduction later

Past reproduction changes future rates

Same age — the same demographic individual this year?



Schematic; the measured differences were half an egg to almost one egg (Slide 9)



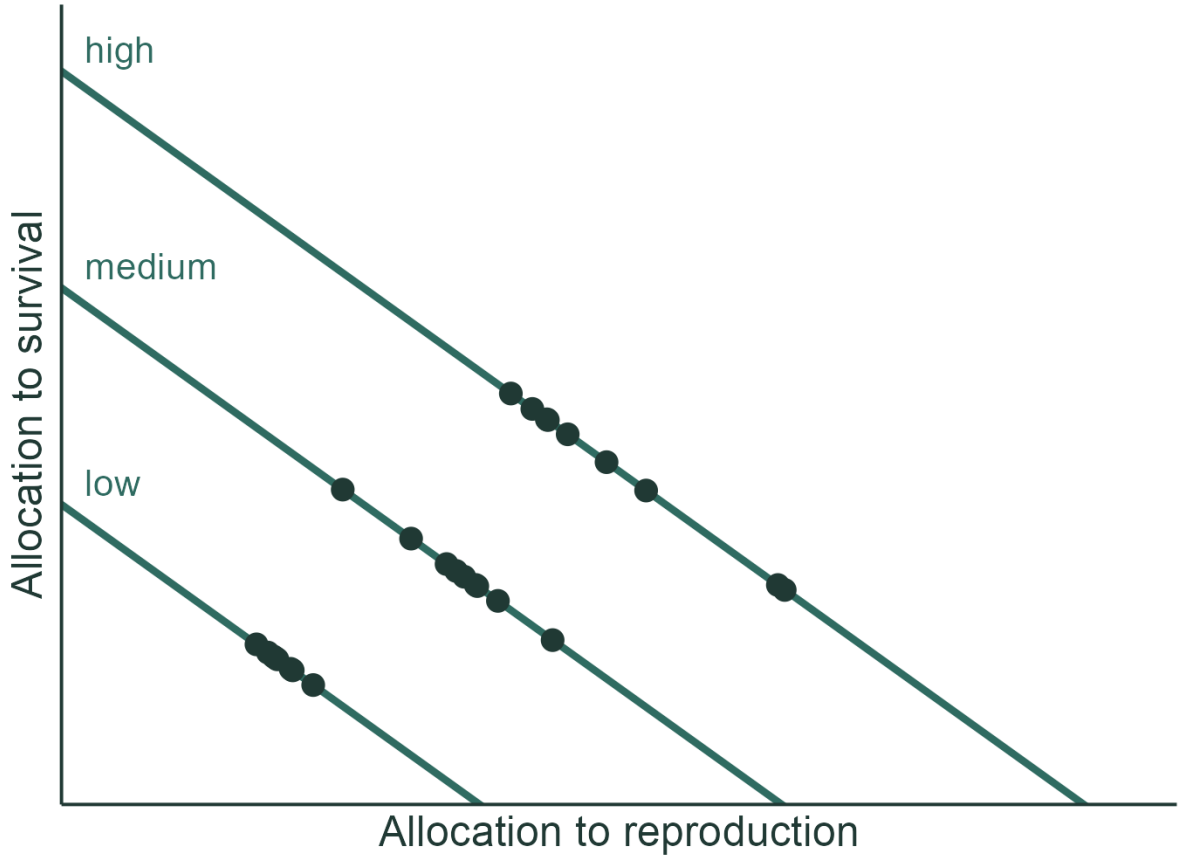
An adult female raising kittens and one without: same age, same demographic state?

Reproductive history and condition can become demographic states.

Superfleas: why trade-offs can hide

Some *Daphnia* lines matured earlier, grew faster and reproduced more.

Did they escape the trade-off?



Lines: resource budgets · illustrative, after Reznick et al. 2000

Within each budget: more to reproduction leaves less for survival.

Across individuals: more resources raise both.

Differences in acquisition can hide allocation costs — and make individuals differ.

Fast and slow lives

Where do the vole, the elephant and the salmon sit?



early maturity
short generation time
many offspring

faster ⟷ **slower**



Late maturity, but one huge burst of reproduction: fast or slow?

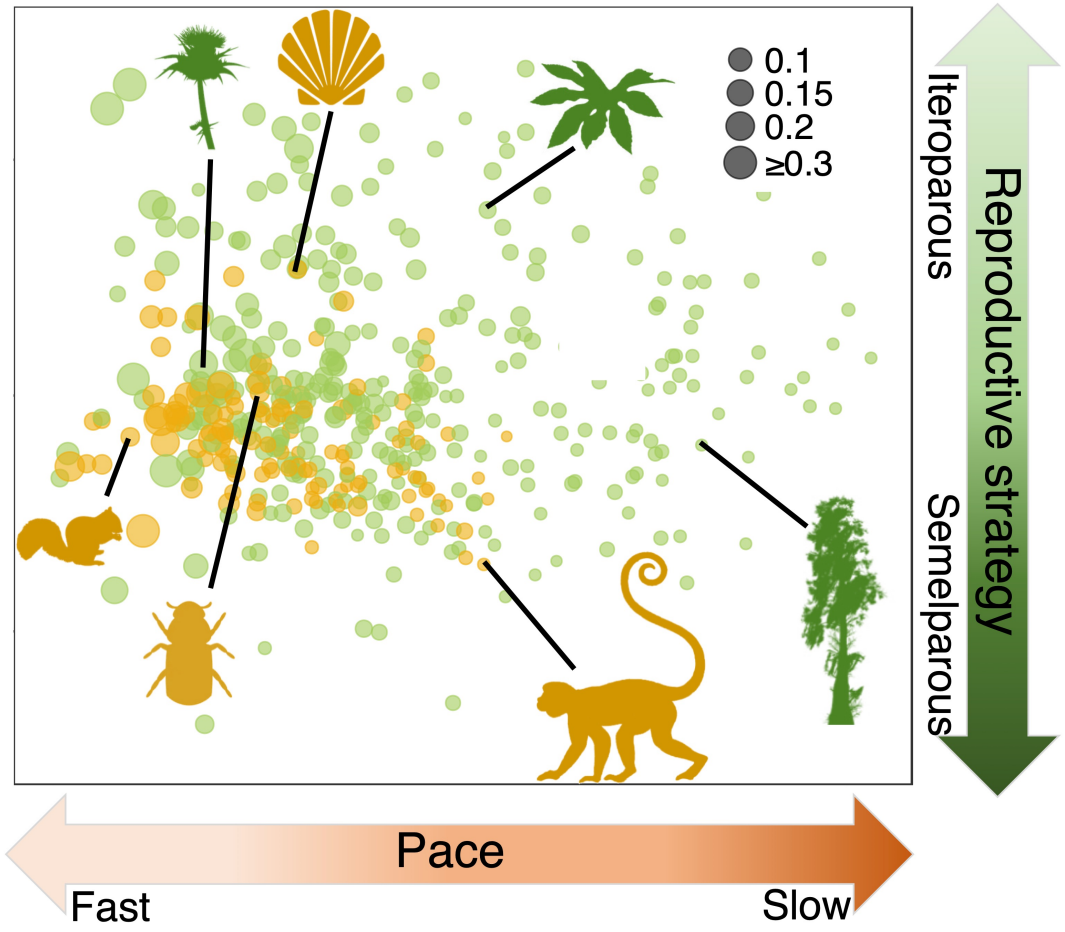


late maturity
long generation time
few offspring, long life

Historical r–K account: selection at low versus high density produced these bundles. Not a general explanation.

Life histories vary along more than one axis

Where would the salmon sit now?



Paniw, Ozgul & Salguero-Gómez 2018, Ecology Letters

454 plant and animal populations

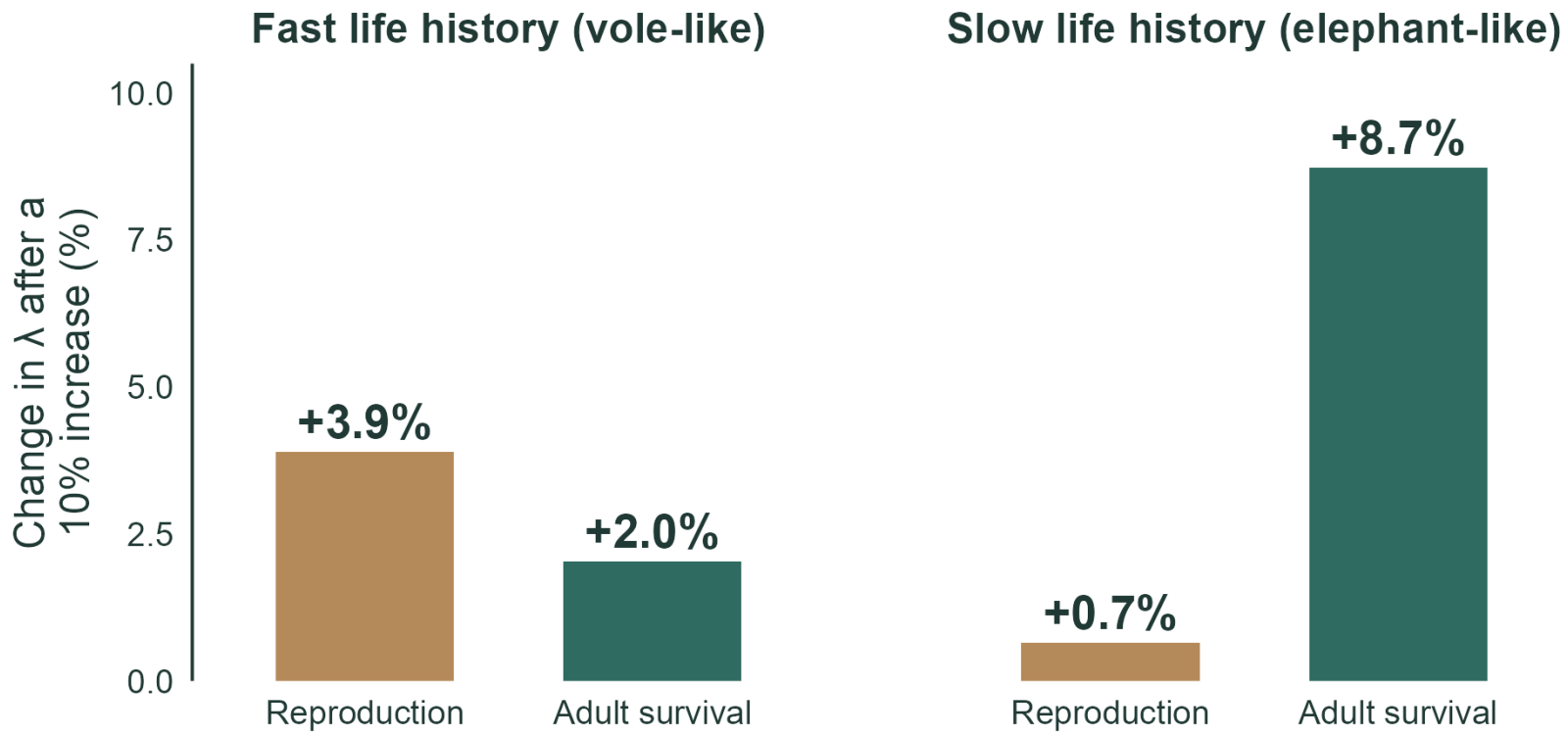
Pace: fast ↔ slow

Reproductive strategy: iteroparous ↔ semelparous

A similar pace can hide very different reproductive schedules.

Life history decides which rates matter

Raise one vital rate by 10%. Which raises population growth more: reproduction or adult survival?



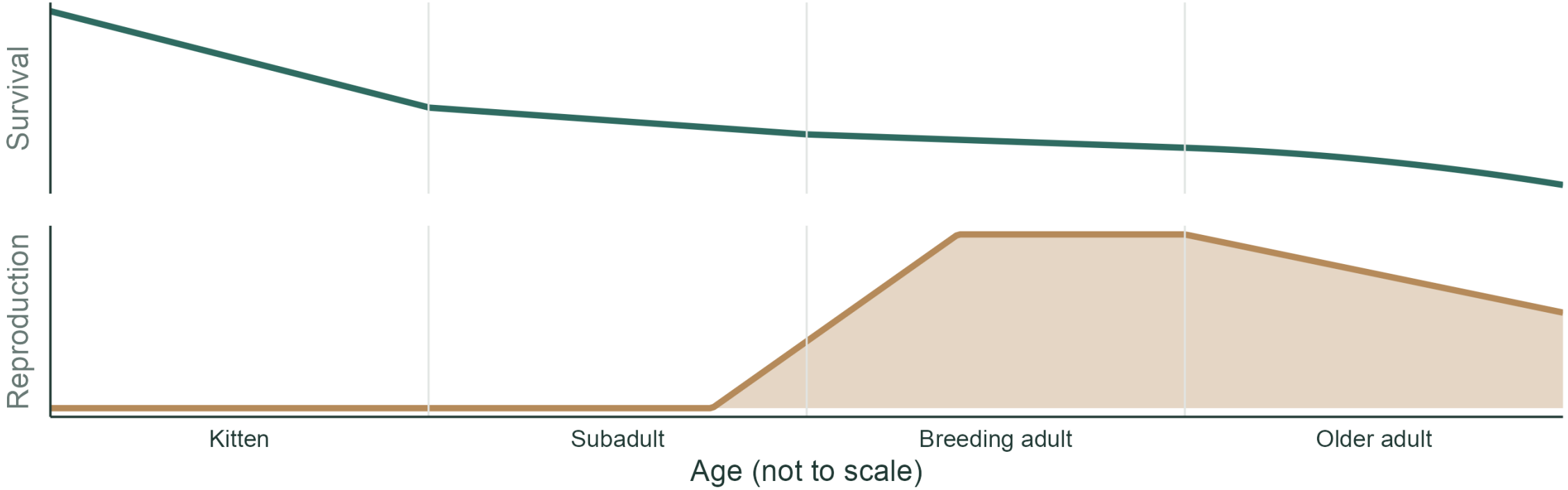
Illustrative two-stage life histories; λ ≈ 1.04 (fast) and 1.01 (slow)

The panther's life schedule

How do survival and reproduction change across a panther's life?





Reproductive value

Kitten, young breeder or old adult: who contributes most to the future?



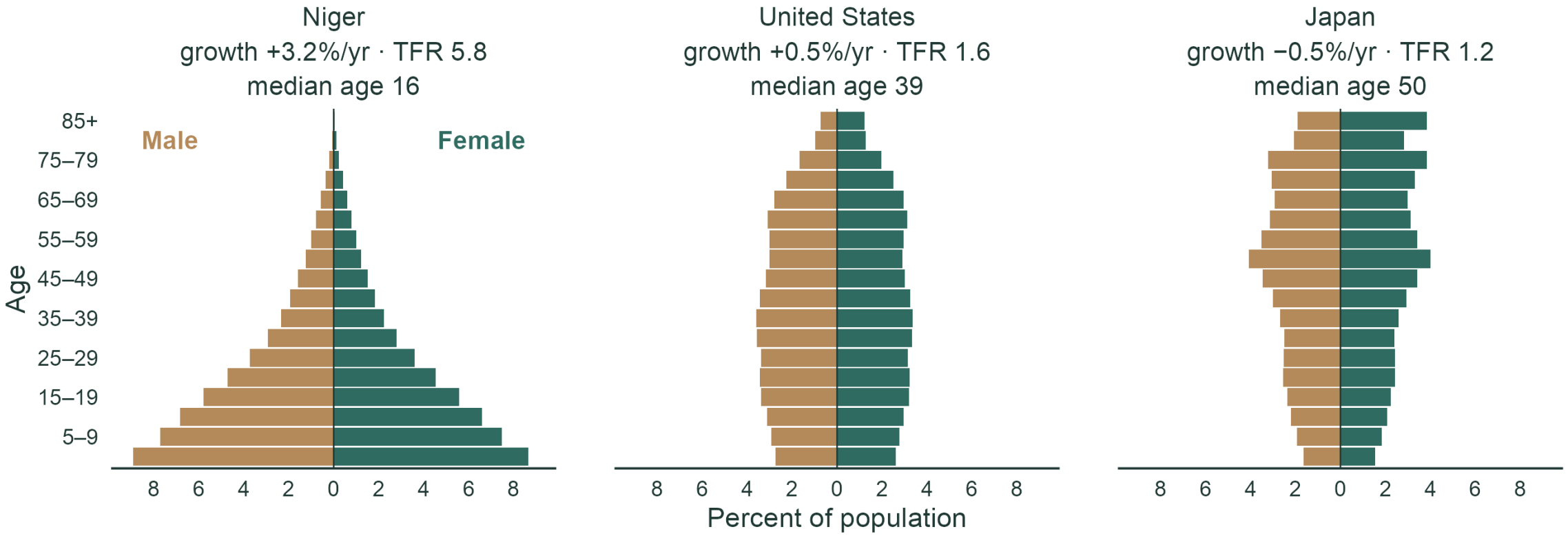





Reproductive value: the expected contribution of an individual in a given state to future population growth.

Structure carries the future

If Niger's fertility fell to replacement level tomorrow, would its population stop growing?

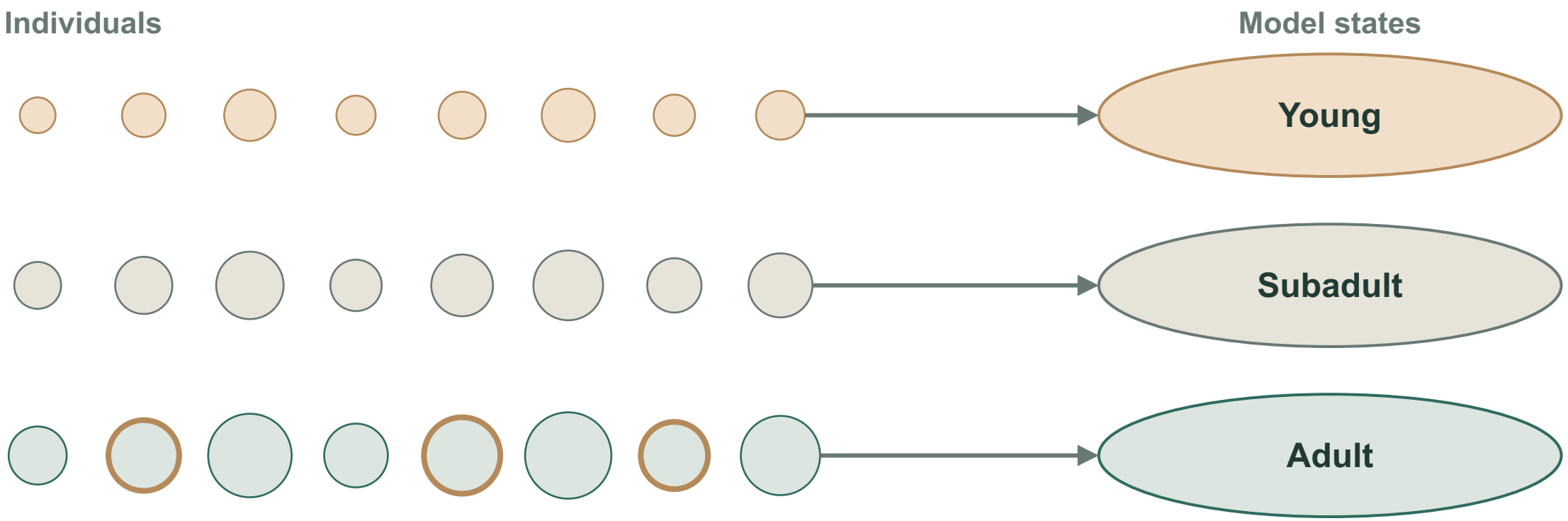


Age structure in 2025 · UN World Population Prospects 2024

Structure reflects past vital rates — and shapes future growth.

Every state model is a simplification

Within each age or stage, individuals still differ: in size, condition, reproductive history, acquisition.



Thick tan outline: reproduced last year

Which differences must the model keep, and which can it combine?

Ideal states

If you could observe every individual, which states would you define?



Florida panther

- Kittens depend on their mother for more than a year.
- Females first breed at about 2 years, males at about 3.
- Females older than 10 rarely raise a litter.



Common frog

- Each female lays one clump of eggs a year, in a pond.
- Tadpoles become froglets in their first summer.
- Froglets live on land for several years before breeding; the shorter the summers, the longer they take.

States the data allow

Which of your states can you still recognise and estimate in the field? Which would you merge?



Florida panther

- Adults are radio-collared; collared females show when they breed.
- Kittens are tagged at the den, then seen again only if caught or found dead.
- Untagged panthers are aged from tooth wear.



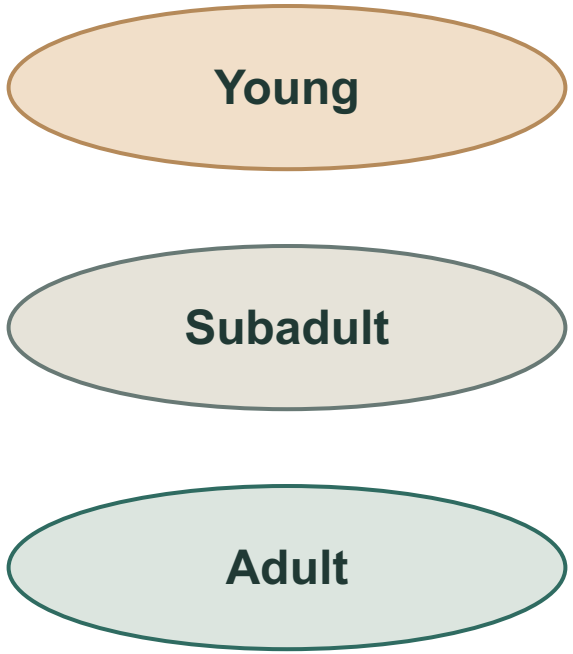
Common frog

- Egg clumps are counted; eggs and tadpoles cannot be marked.
- Froglets disperse on land and are rarely found again.
- Only adults that come to breed are caught; age needs a toe bone.

From life histories to model states

What did we learn today?

- A life history is a schedule of survival and reproduction; fitness depends on timing, not just number.
- Trade-offs make individuals of the same age demographically different.
- Life history decides which vital rates most influence growth.
- Today's composition reflects past rates and shapes future dynamics.
- Choose the simplest states that keep the differences that matter and can be estimated.



Given these states, how do individuals survive, reproduce and move among them?

Further reading



Journal of Animal Ecology 1996, 65, 539–544

Increased daily work precipitates natural death in the kestrel

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Summary

1. Costs of reproduction have been assessed experimentally by measuring subsequent survival and reproduction of parent animals raising enlarged and reduced numbers of offspring. Reported effects on survival have so far always referred to local survival of marked individuals in the study population. They do not provide definitive proof of a cost of reproduction, since reduced local survival may be due either to reduced survival or to an increased tendency to emigrate from the study area. Therefore, it is important to assess mortality rates in connection with brood size experiments

2. We report an analysis of the time of death in 63 cases where kestrels, *Falco tinnunculus* L. had raised broods of manipulated size and were subsequently reported freshly dead. 60% of the parents raising two extra nestlings were reported dead before the end of the first winter, compared to 29% of those raising control or reduced broods. This result confirms our interpretation of the manipulation effects on local survival as due to mortality rather than emigration. The extra mortality occurred in the winter following the brood enlargement

3. Kestrel parents in these experiments have been shown to adjust their daily energy expenditure to the modified brood size. Increased parental effort in this species thus entails an increased risk of death half a year later.

Key-words: brood size manipulation, cost of reproduction, dispersion, recoveries, survival

Journal of Animal Ecology (1996), **65**, 539–544

Introduction

A reduction in the residual reproductive value of parents as a consequence of their reproductive effort, as postulated first by Williams (1966), is one of the central theorems of life-history theory. This cost of reproduction in iteroparous animals leads to a trade-off between the number of offspring in the current brood (brood size) and expected future reproduction, and forms the basis of clutch size theory (Charnov & Krebs 1974). A cost of reproduction may be found in subsequent fecundity or in subsequent survival or in both. The method to evaluate such costs has generally been the manipulation of the number of young after birth of a litter or brood, and the subsequent assessment of survival and/or fecundity of individually marked parents in the study population. The most elementary effects on subsequent fecundity have been those where the incidence of second broods was reduced following enlargement, or enhanced following reduction of the first brood (Smith, Kilfander & Nilsson 1987; Lindén 1988; Tinbergen 1987; Verhulst 1995; Verhulst & Hut 1996). In addition, long-term effects on reproductive success have been observed (Gustafsson & Sutherland 1988; Ruskaft 1985; Verhulst 1995). Effects on fecundity may be viewed either as a physiological or as a strategic consequence of the experiment. For instance, the effects may be in the first place on a physiological condition affecting the probability of survival, which might alter the strategic decision of the animals whether or not to produce another brood.

Effects of brood size manipulations on survival itself have been less unambiguously demonstrated. Such effects have so far been reported in three species (*Ficedula hypoleuca* Askenmo 1979; *Parus caeruleus* Nur 1984, but see Pettifor 1993; *Falco timnunculus* Dijkstra *et al.* 1990). In all cases the data refer to *local survival*, i.e. the relative frequency of return to the next breeding population of individually marked parents. Decreased local survival may reflect increased mortality or an increased tendency to leave the local area, or a combination of both. Increased emigration is a plausible alternative hypothesis for birds for whom reproduction has been more exhaustive, and which

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ONE PAPER

Daan, Deerenberg and Dijkstra (1996), *Journal of Animal Ecology*
Kestrels raising enlarged broods: does extra work cost survival?

Focus: the Introduction (lower local survival: death or leaving?), Table 1, Fig. 1 (survival by treatment).

Skip: the deviance tables (Table 3). Fig. 2 has no symbol key: read it with the text.

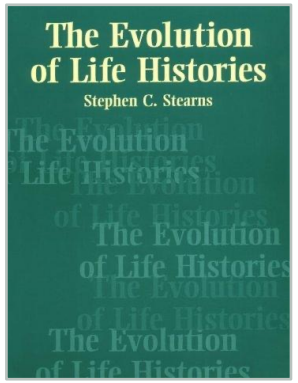
Later: the Introduction again after L10: local survival is apparent survival.

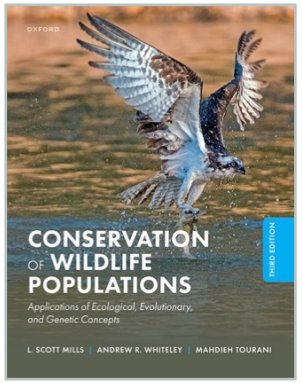
RESOURCES

Mills, Whiteley and Tourani (2025), Conservation of Wildlife Populations, Ch. 6: fitness, states and reproductive value.

Stearns (1992), The Evolution of Life Histories: life-history schedules and trade-offs.

Stearns' lecture on evolutionary trade-offs: watch online.

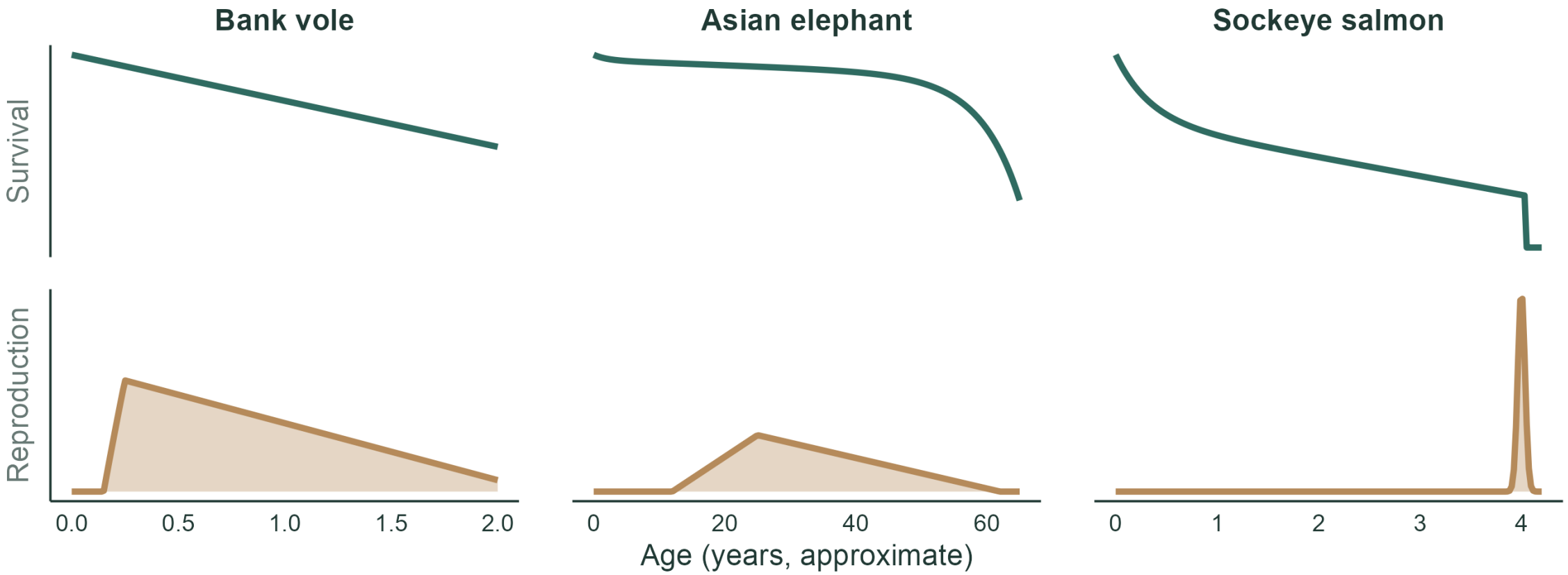




Answers

EEE330 · Lecture 2

Contrasting lives



Illustrative schedules; survival on a log scale

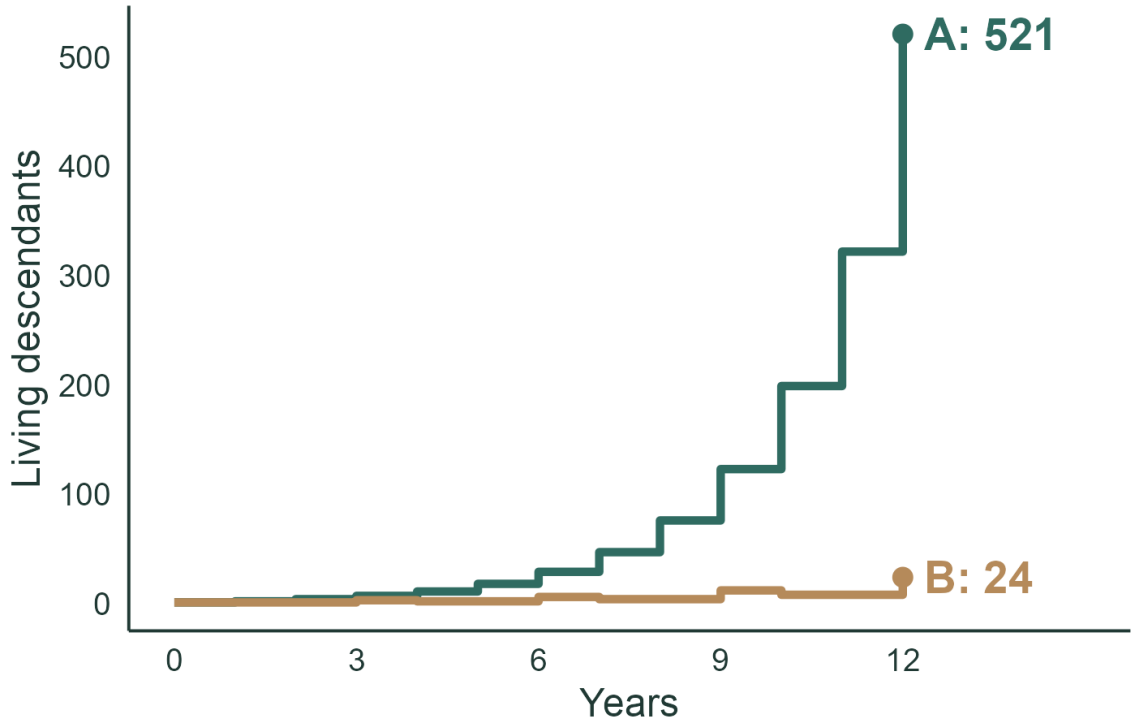
Life history: the schedule of survival, growth and reproduction across life.

‹ Question

Two genotypes, two schedules

Two genotypes. Everyone survives to age 3, then dies. Both produce 2 offspring in a lifetime.

Age	1	2	3
Genotype A	1	1	0
Genotype B	0	0	2



Calculated: offspring inherit the schedule; no density dependence

Equal lifetime output, unequal fitness: timing matters.

‹ Question

Four summaries of fitness

	LRS	R_0	T	λ
A	2	2	1.5	1.62
B	2	2	3	1.26

$$\lambda \approx {R_0}^{1/T}$$

The same output per generation, delivered faster, grows faster.

LRS: lifetime reproductive success · R_0: expected offspring per generation · T: mean age of reproduction · λ: growth factor per year

‹ Question