

The **queen** and the demon

Concepts of directionality in evolution



Marcus Clauss

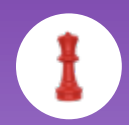
Zürich, EvoBio554 2020



University of
Zurich^{UZH}



Clinic
of Zoo Animals, Exotic Pets and Wildlife



Many evolutionary biologists
abhor the concept of
directionality
in evolution.



1.60m
Equus Caballus



Around 10 million years ago, horse species that maintained a fruit and leaf diet became extinct, and about 4-5 million years later species that had intermediate diets (part leafy and part grassy) also disappeared. Only the grass-eating equids that eventually became the modern day horse (*Equus ferus caballus*) survived.

Recent
1 million years ago



1.25m
Pliohippus



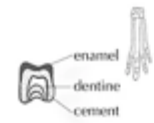
tooth completely covered with cement



1m
Merychippus



0.6m
Mesohippus



0.4m
Hyracotherium



Late Miocene
8 million years ago

Middle Miocene
15 million years ago

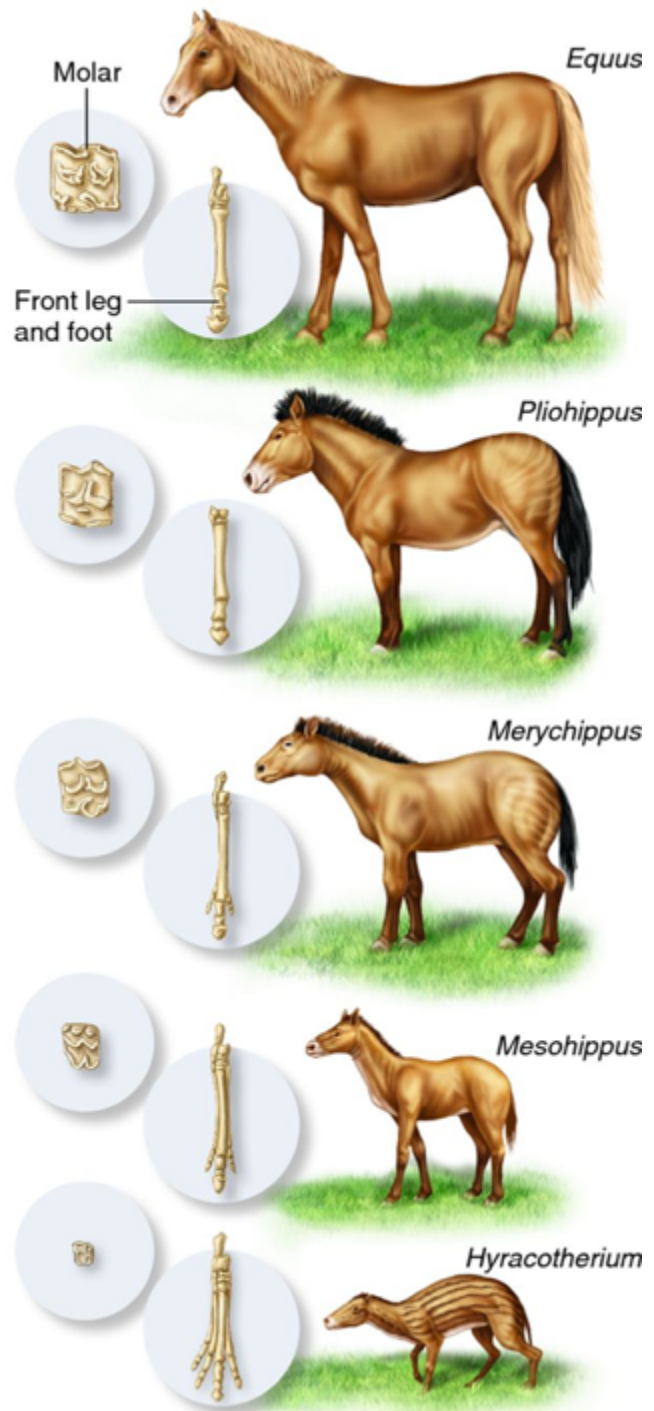
Late Eocene
35 million years ago

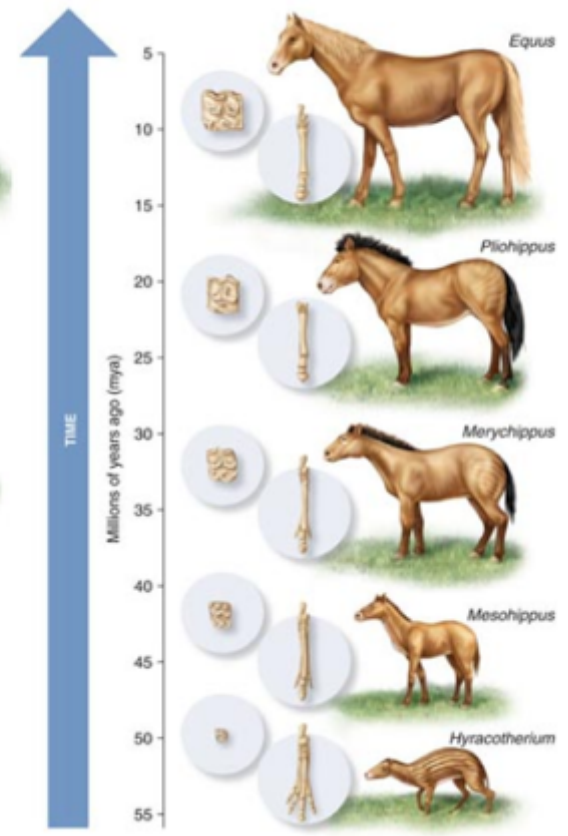
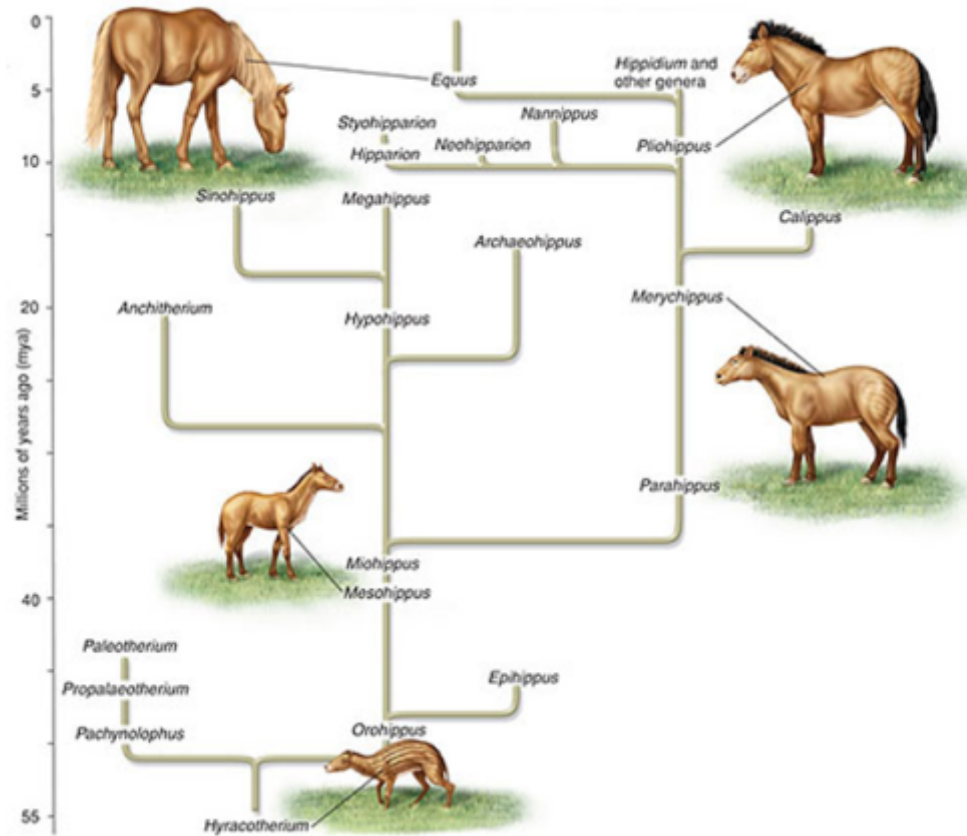
Early Eocene
55-60 million years ago

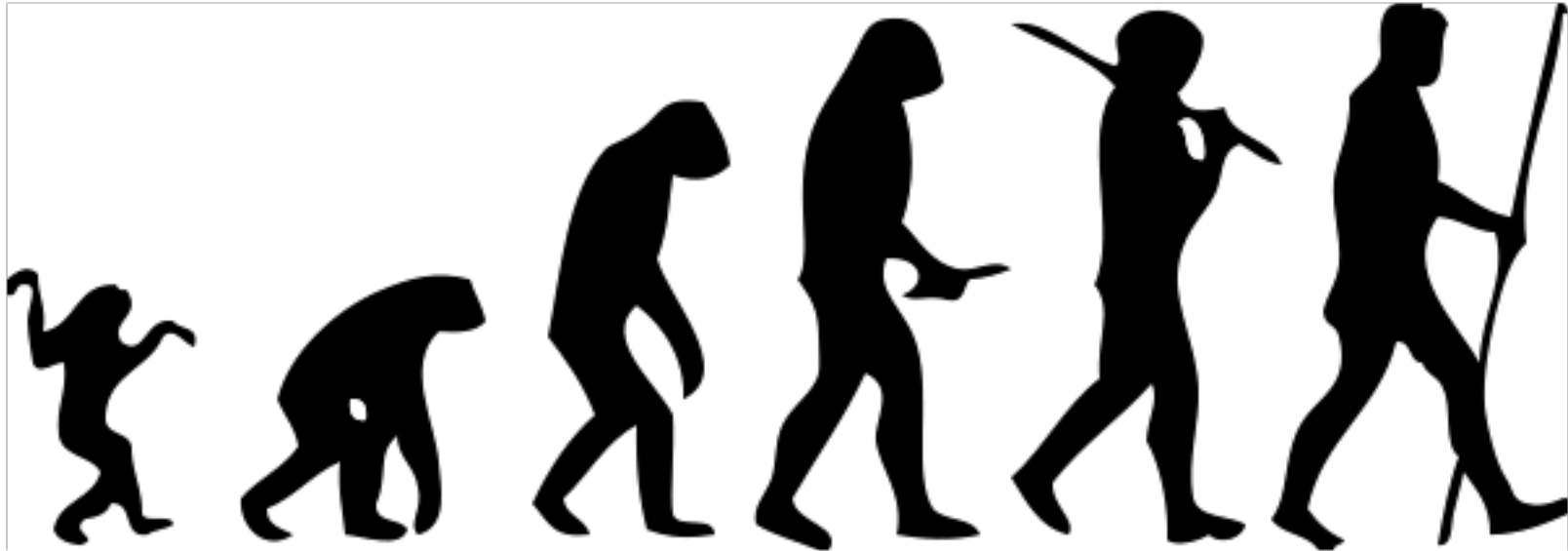


Millions of years ago (mya)

5
10
15
20
25
30
35
40
45
50
55







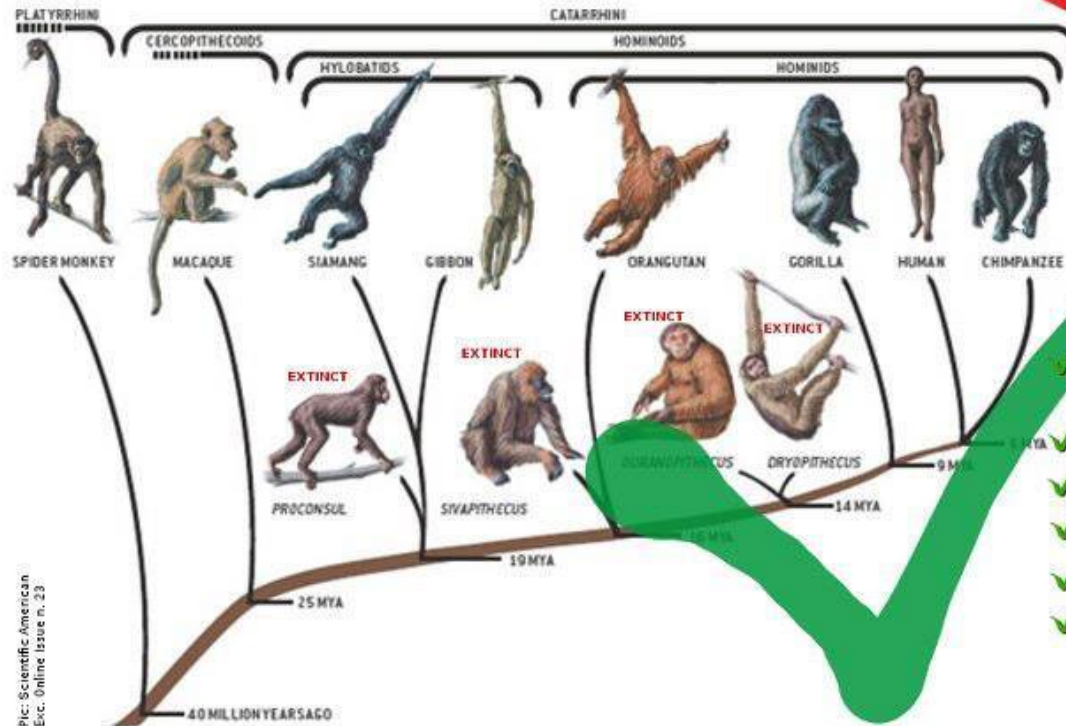
THIS IS NOT EVOLUTION

- This is *Scala Naturae*, an incorrect pre-evolutionary concept
- ⊘ Suggests progress, not adaptation
- ⊘ Human is a target, superior being
- ⊘ Ancestor being resembles a chimp
- ⊘ No branches or extinctions



THIS IS NOT EVOLUTION

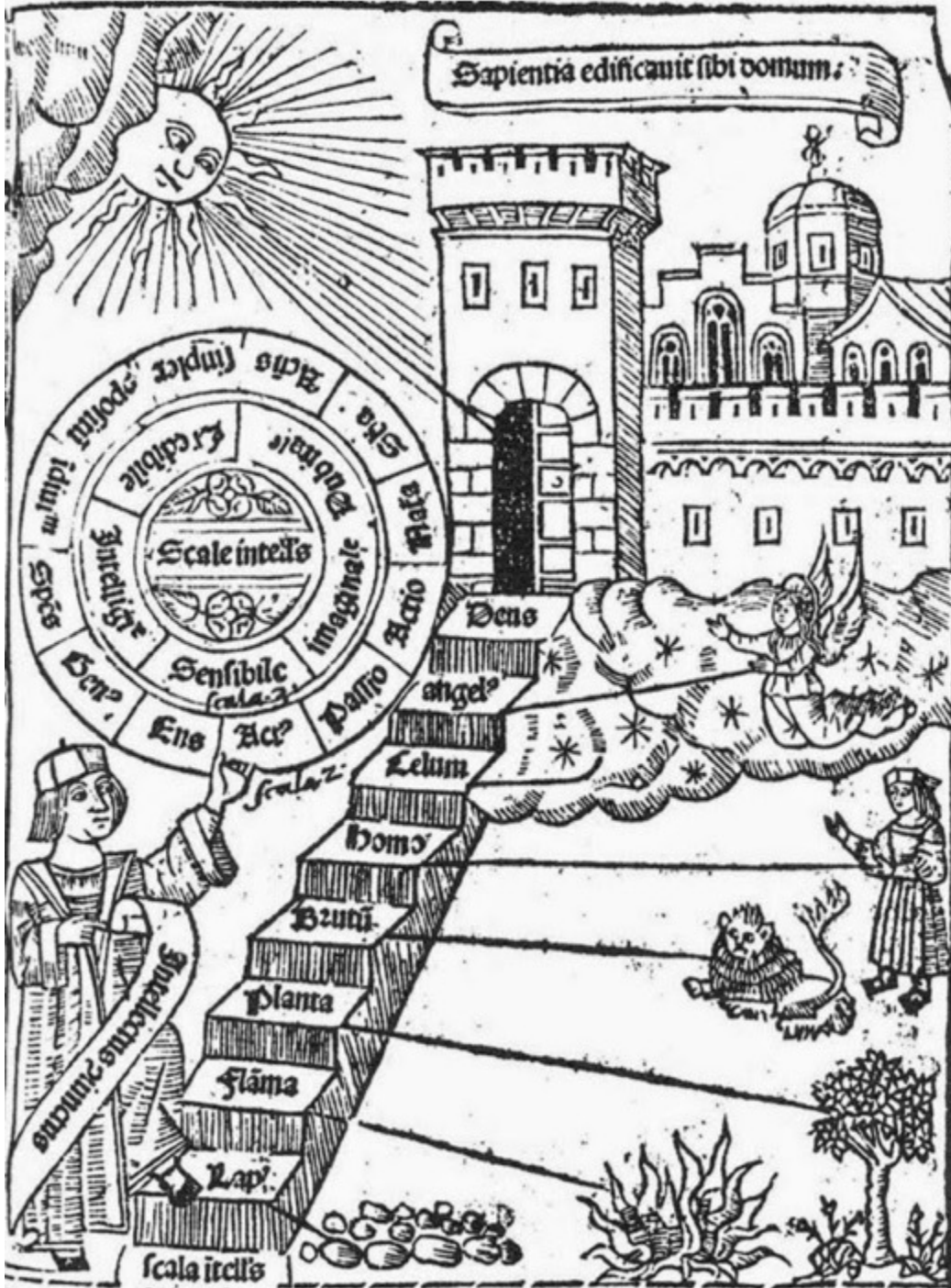
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THIS IS EVOLUTION

- ✓ Humans are not special. Just a species, not superior, "more evolved" or a target.
- ✓ Some species become extinct (99% of them)
- ✓ Chimps are not portrayed as ancestors
- ✓ Individual beings do not change. Populations do
- ✓ Ancestor species branches into other species
- ✓ Adaptations might lead to smaller size, loss of unused features and extinction

Sapientia edificavit sibi domum.



PHILOSOPHIE ZOOLOGIQUE, ou EXPOSITION

Des Considérations relatives à l'histoire naturelle des Animaux ; à la diversité de leur organisation et des facultés qu'ils en obtiennent ; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils exécutent ; enfin , à celles qui produisent , les unes le sentiment , et les autres l'intelligence de ceux qui en sont doués ;

PAR J. - B. - P. - A. LAMARCK ,

TOME PREMIER.

A PARIS ,

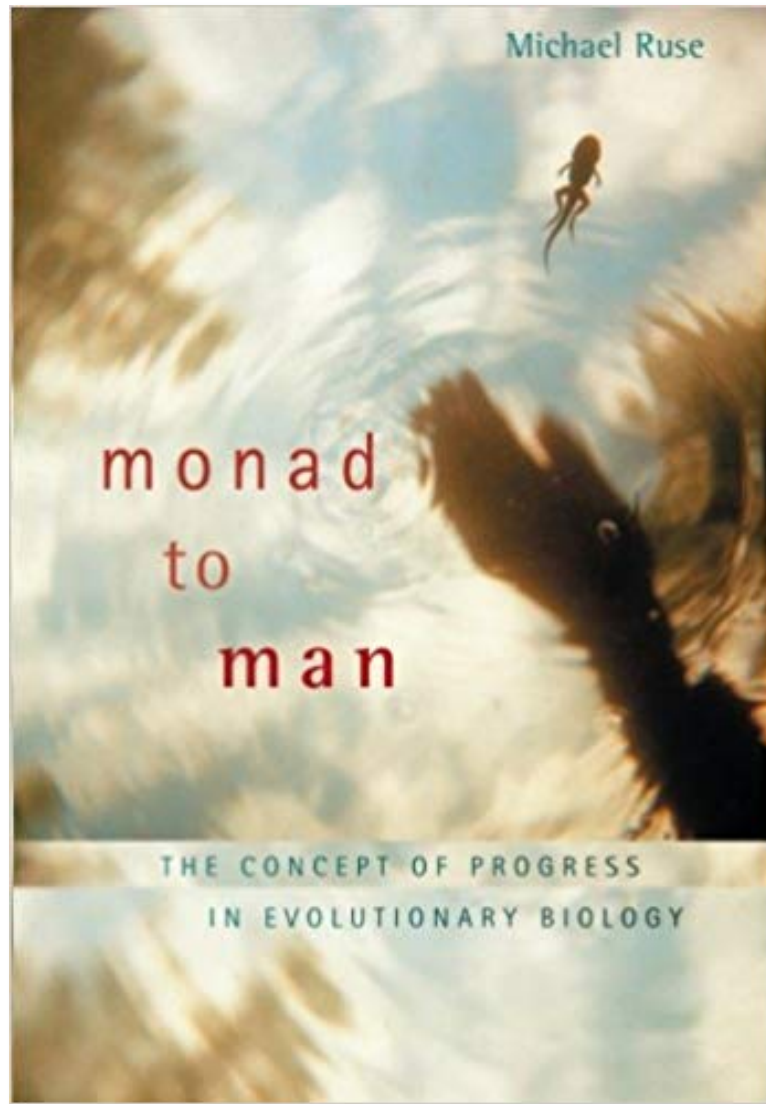
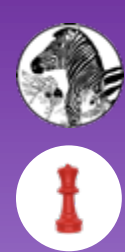
{ DENTU, Libraire, rue du Pont de Lodi, N°. 3 ;
Chez L'AUTEUR, au Muséum d'Histoire Naturelle (Jardin
des Plantes).

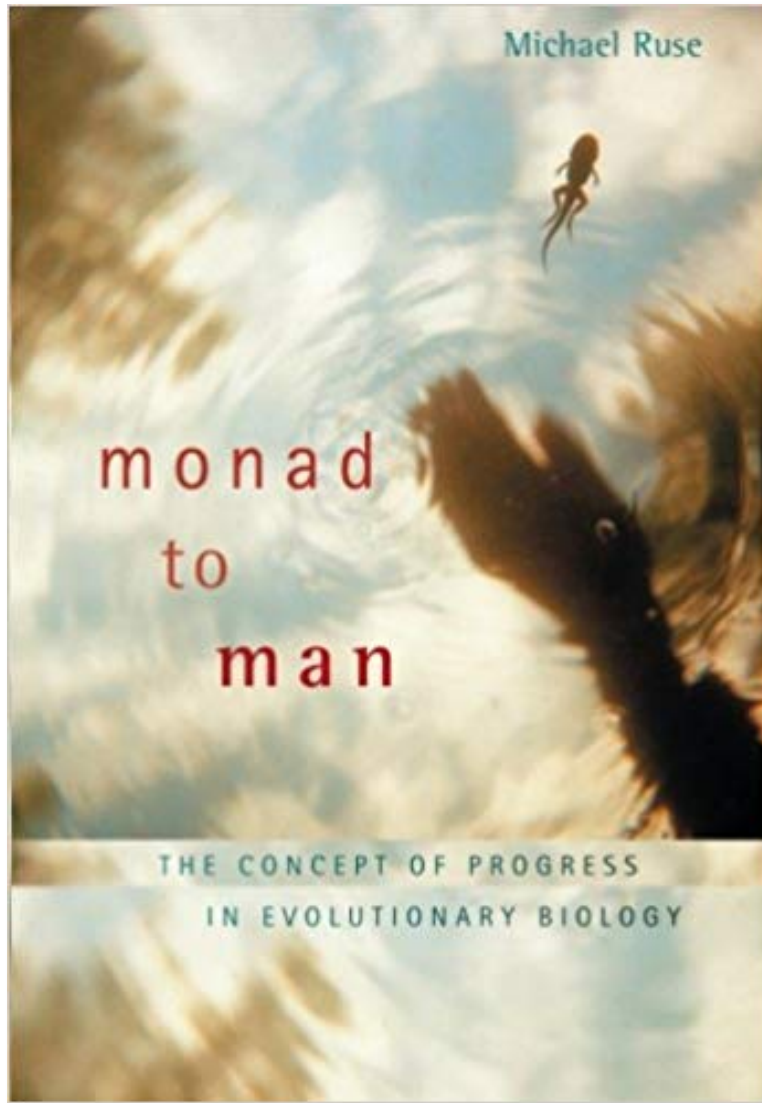
M. DCCC. IX.

IDÉE D'UNE ÉCHELLE

DES ETRES NATURELS.

L'HOMME.
Orang-Outang.
Singe.
QUADRUPÈDES.
Écureuil volant.
Chauve-souris.
Autruche.
OISEAUX.
Oiseaux aquatiques.
Oiseaux amphibies.
Poissons volans.
POISSONS.
Poissons rampans.
Anguilles.
Serpens d'eau.
SERPENS.
Limaces.
Limaçons.
COQUILLAGES.
Vers à tuyau.
Teignes.
INSECTES.
Gallinules.
Ténia, ou Solitaire.
Polypes
Orties de Mer.
Sensitive.
PLANTES.





Stephen Gould



... my favourite theme that Darwinian evolution cannot be read as a theory of progress, but only as a mechanism for building better adaptation to changing local environments - and that the equation of evolution with progress represents our strongest cultural impediment to a proper understanding of evolution



Our failure to find any clear vector of [...] accumulating progress [...] represents our greatest dilemma for a study of patterns in life's history.



'Evolutionary progress' – directional evolution

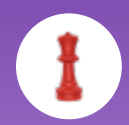
Biol. Rev. (1987), **62**, pp. 305–338

PROGRESS AND COMPETITION IN MACROEVOLUTION

By MICHAEL J. BENTON

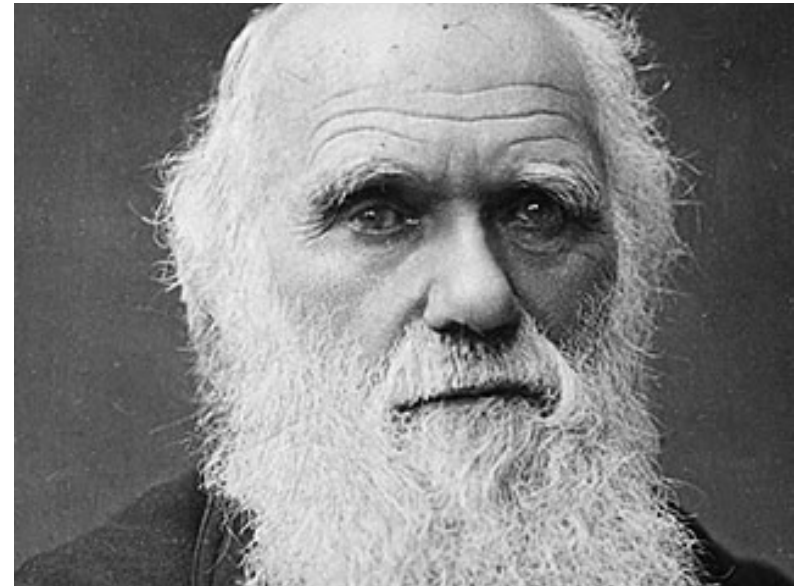
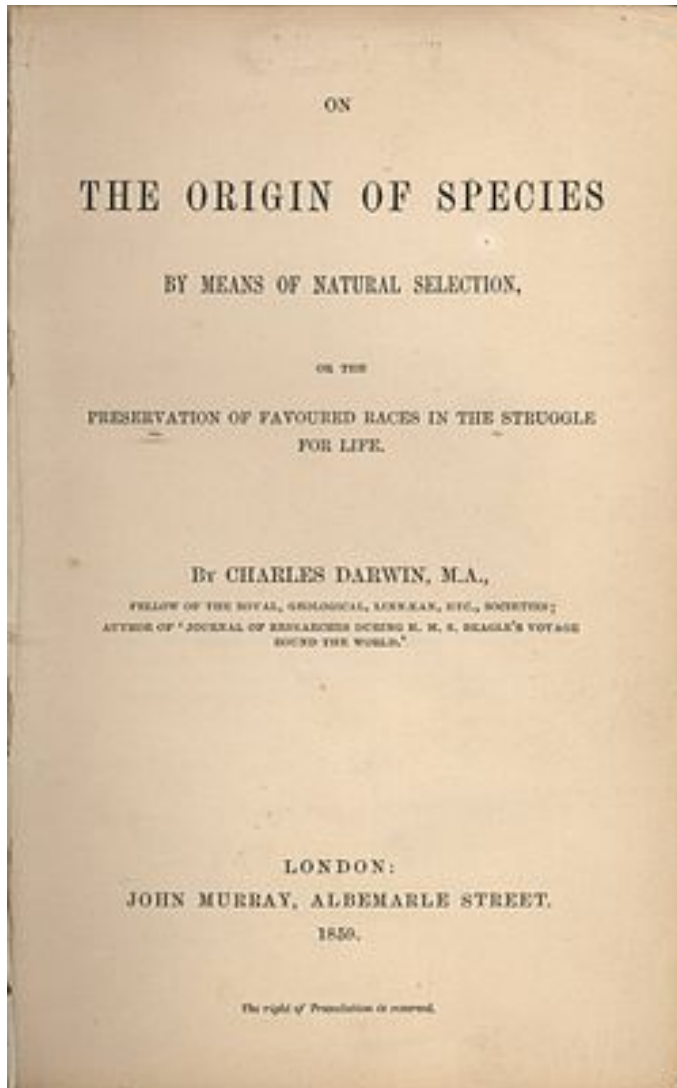
It is merely a tautology to identify the later animal (the 'winner') as a 'superior competitor' in the absence of any other evidence (Schopf, 1979).

it is hard to envisage a constant competitive advantage that lasted so long and persistently favoured all of the species of one large taxon against all of the species of another in all environments.



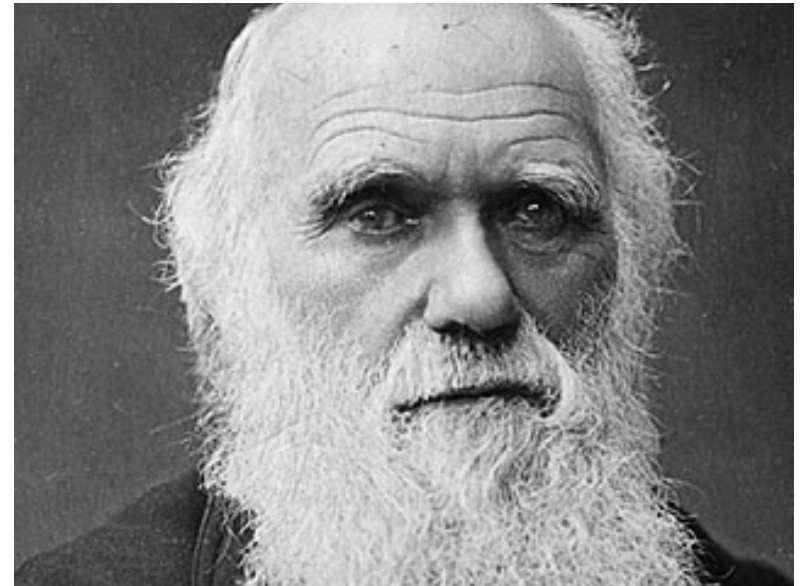
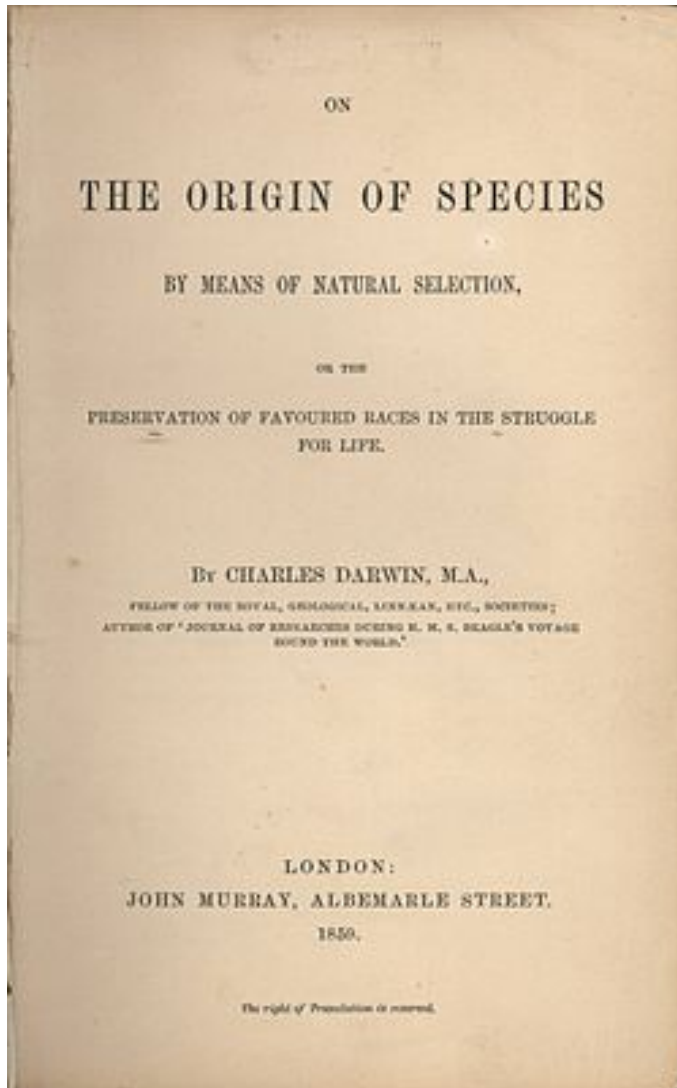
Darwinian evolution is a set of rules where the one constant (demographic) selective pressure is to outreproduce competitors.

‘Evolutionary progress’ – directional evolution



"The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life [...] and this may account for that vague yet ill-defined sentiment [...] that organization on the whole has progressed"

‘Evolutionary progress’ – directional evolution



"as natural selection works solely by and for the good of each being, all corporal and mental endowments will tend to progress towards perfection"

PHILOSOPHIE ZOOLOGIQUE, ou EXPOSITION

Des Considérations relatives à l'histoire naturelle des Animaux ; à la diversité de leur organisation ; et des facultés qu'ils en obtiennent ; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils exécutent ; enfin , à celles qui produisent , les unes le sentiment , et les autres l'intelligence de ceux qui en sont doués ;

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Polypes
Orties de Mer.
Sensitive.
PLANTES.

Evolutionary Ecology Research, 2013, 15: 747–756

Cope's Law of the Unspecialized, Cope's Rule, and weak directionality in evolution

Pasquale Raia¹ and Mikael Fortelius²

Understanding of directionality was akin to Lamarck's concept of linear progress up life's ladder, and ever since the many evils of social Darwinism were recognized and abandoned, evolutionary biologists have been extremely cautious about considering evolutionary progress of any sort.



A NEW EVOLUTIONARY LAW

Leigh Van Valen

The Red Queen's Hypothesis (32)

(32). "Now here, you see, it takes all the running you can do, to keep in the same place." (L. Carroll, Through the Looking Glass.)

Evol. Theory 1:1-30 (July 1973)



‘Evolutionary progress’ – directional evolution



The crab is the natural predator of the snail.



Natural selection favors snails with thicker shells and spines.



Through natural selection, crabs evolve more powerful claws that can pierce the snails' thick, spiny shells.

In response, natural selection favors snails with even thicker shells and spines.





‘Evolutionary progress’ – directional evolution

Proc. R. Soc. Lond. B **205**, 489–511 (1979)

489

Printed in Great Britain

Arms races between and within species

BY R. DAWKINS AND J. R. KREBS

reverse as to continue the previous one. But in fact consistent directionality is introduced because the environment of any one evolving lineage includes other evolving lineages. Above all, it is because adaptations in one lineage call forth counter-adaptations in others, setting in motion the unstable evolutionary progressions we call arms races.





BE NICE TO FAT PEOPLE

ONE DAY THEY MAY SAVE YOUR LIFE

The best way to survive a polar bear attack is to go for a walk with a friend that you can outrun!



your  cards
someecards.com

You don't have to outrun the bear—
you just have to outrun the other campers.



SPIRIVA[®] RESPIMAT[™]
(tiotropium bromide) INHALATION SPRAY

**SPIRIVA.
DON'T BECOME
BEAR FOOD**

**ALWAYS HIKE WITH SOMEONE
IN WORSE SHAPE THAN YOU.**



**THERE'S BEARS OUT
THERE YOU KNOW.**



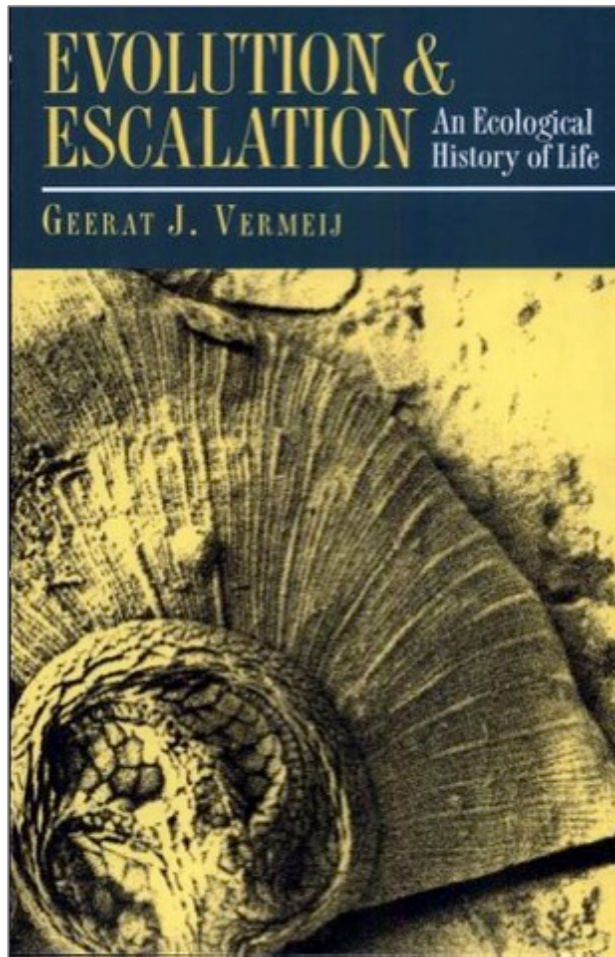
lifetips

You don't need to run
faster than the bear,
you just need to run
faster than the other
guy running from the
bear

**TRAIN SMART, NOT HARD:
YOU DON'T HAVE TO
OUTRUN THE
BEAR.
YOU JUST HAVE TO
OUTRUN YOUR
BUDDIES.**



‘Evolutionary progress’ – directional evolution



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On Escalation

Geerat J. Vermeij

Department of Geology, University of California, Davis, California 95616;
email: gjvermeij@ucdavis.edu



Annu. Rev. Earth Planet. Sci. 2013. 41:1–19

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

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Keywords

Red Queen, coevolution, Phanerozoic, enabling factors, predation, competition

Abstract

Organisms have been important agents of selection throughout the history of life. The processes and outcomes of this selection are the subject of this review. Among these, escalation is the most widespread. The primary selective agents are powerful competitors and consumers, which together push many populations toward higher performance in acquiring and defending resources while relegating less competitive species to physiologically marginal settings, where escalation also ensues. The extent to which performance standards rise depends on enabling factors, which control availability of and access to resources. By establishing positive feedbacks between species and enabling factors, effective competitors regulate and enhance resource supply. The pace of escalation toward greater power and reach is dictated by geological factors as well as by growing interdependencies between species and their resources. Evolutionary events on land related to the production of oxygen may have been instrumental in triggering the major episodes of escalation.





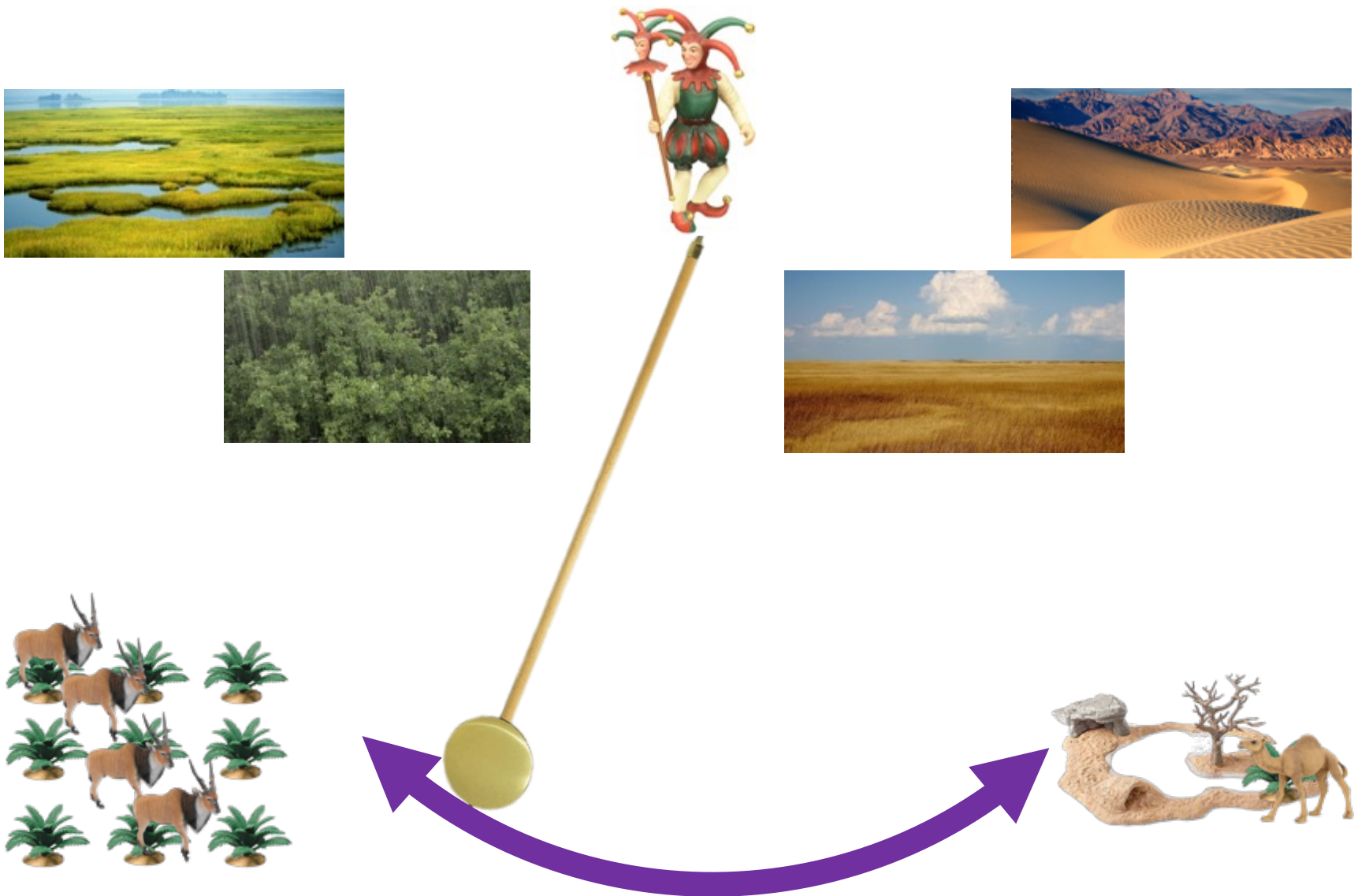
The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time

Michael J. Benton

FEBRUARY 2009 VOL 323 SCIENCE

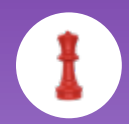


The Court Jester's pendulum



The Court Jester's pendulum





Probabilistic directionality in evolution



A priori conditions and their consequences

Life requires input of resources.

Life starts simple (non-complex).

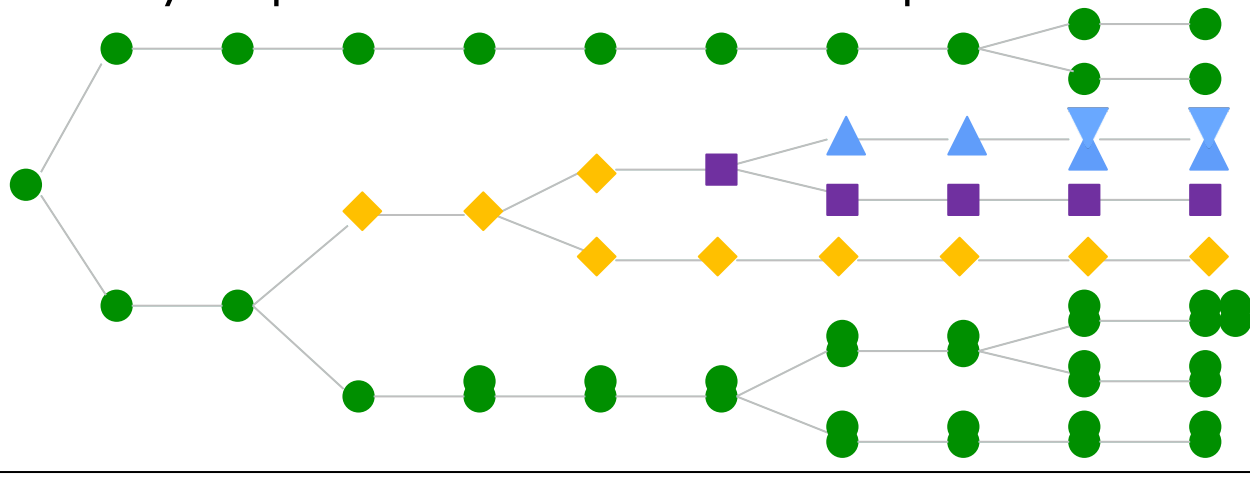
Life means reproduction.

- spontaneously occurring yet heritable variability

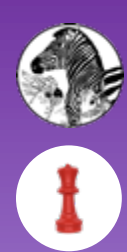


Probabilistic directionality I: towards non-stasis

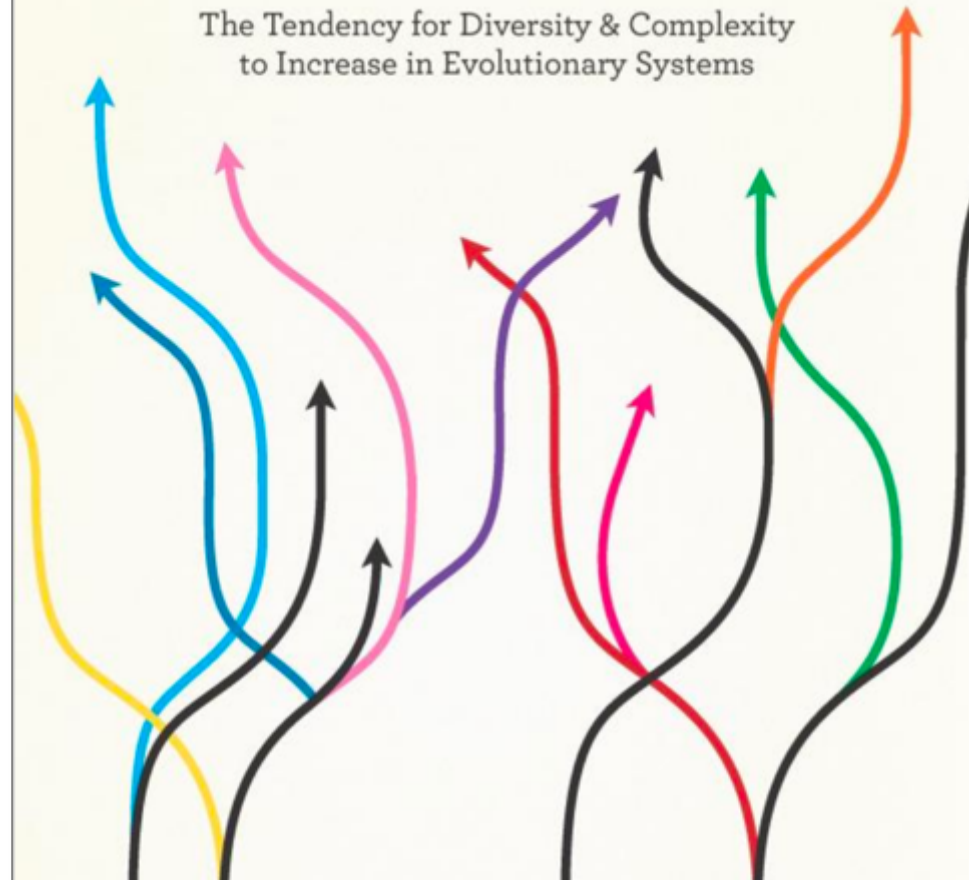
- not only replacement but multiplication



Probabilistic directionality II: more diversity & complexity



The Tendency for Diversity & Complexity
to Increase in Evolutionary Systems

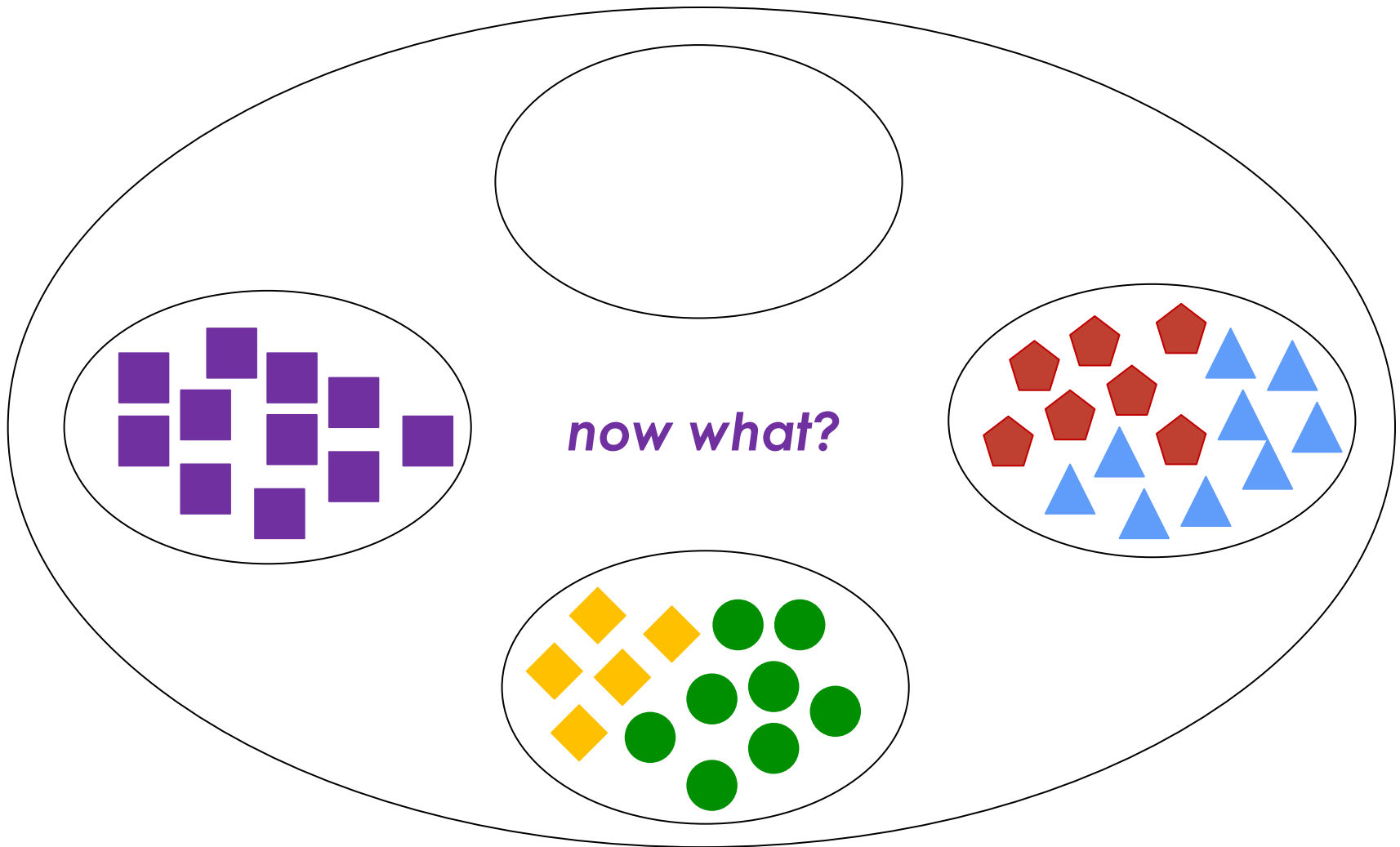


BIOLOGY'S FIRST LAW

DANIEL W. McSHEA & ROBERT N. BRANDON

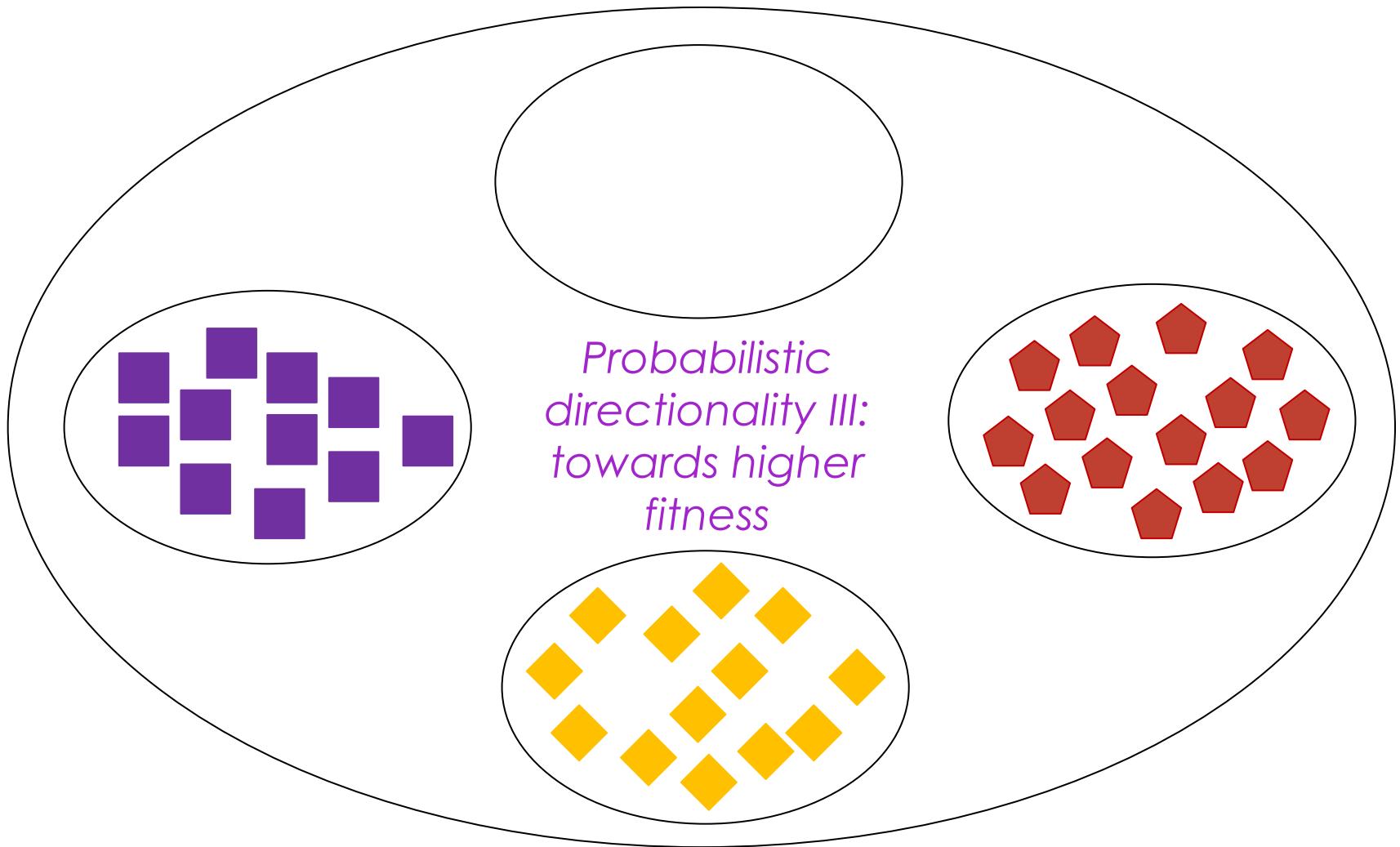
A priori conditions and their consequences

Resources are finite.



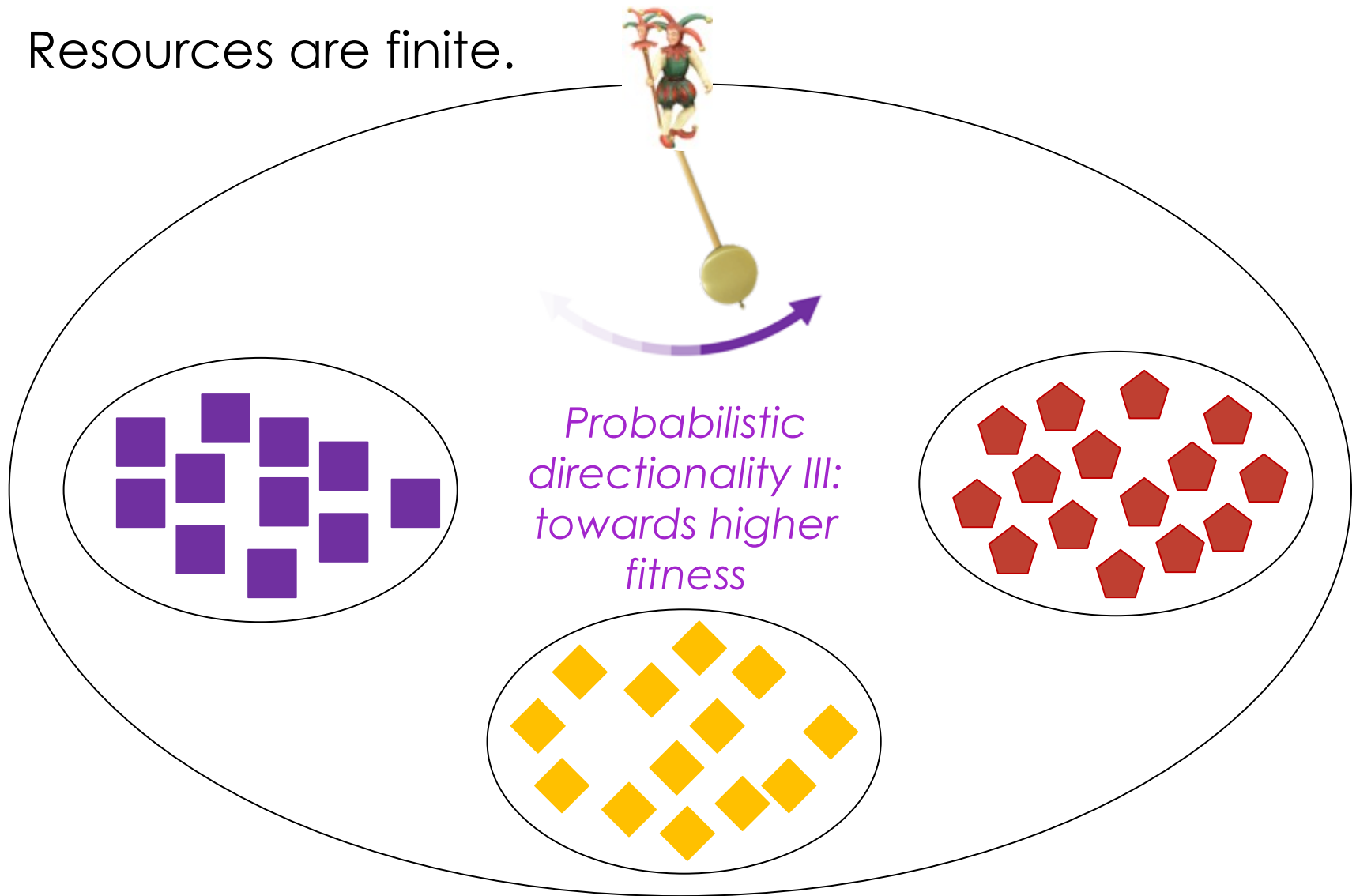
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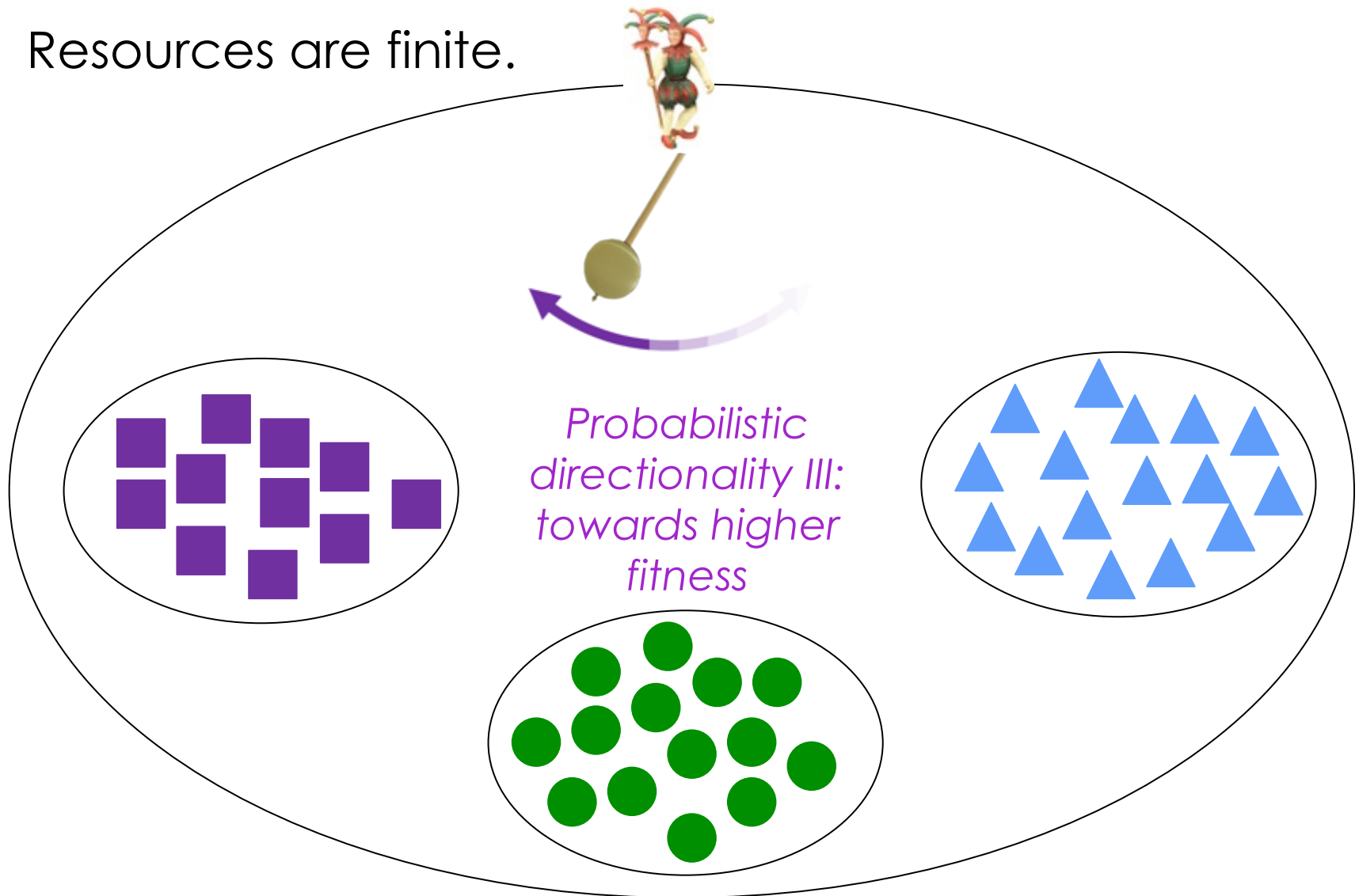
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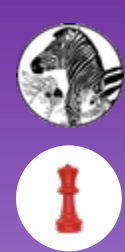
Resources are finite.



A priori conditions and their consequences

Resources are finite.





Court Jester examples ?

'momentary solutions' ← → 'permanent solutions'



Cold-adapted species are replaced
when climate gets warmer.

Unguligrade species are replaced ...
... when global habitats become swamps ?

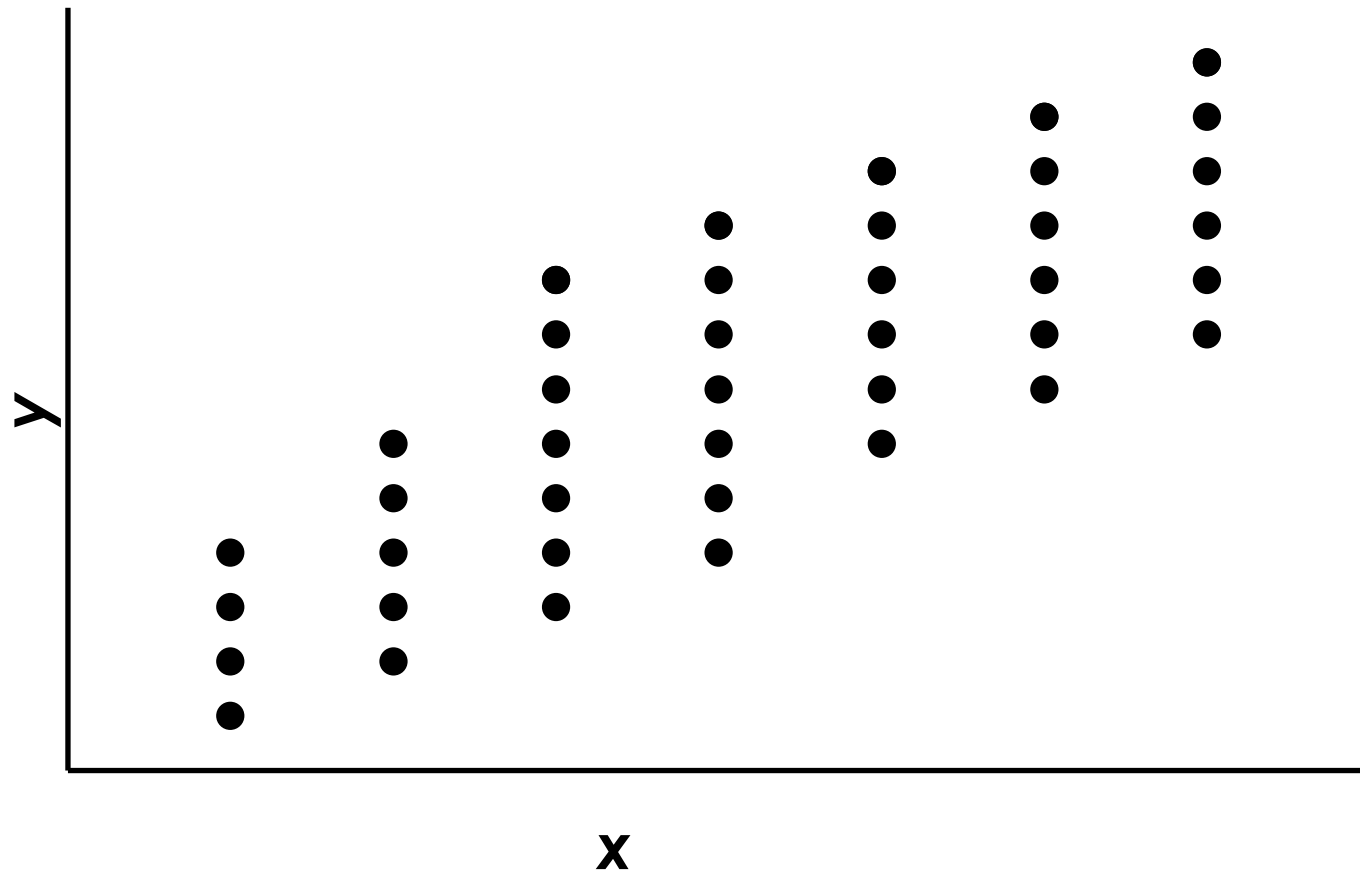
Species with specific anti-predator defences are replaced ...
... when any predators disappear ?

Herbivores with specific adaptations for chewing are replaced ...
... by herbivores with enzymatic plant fibre digestion ?
... when plants dominate that do not contain fibre ?



Interpreting patterns

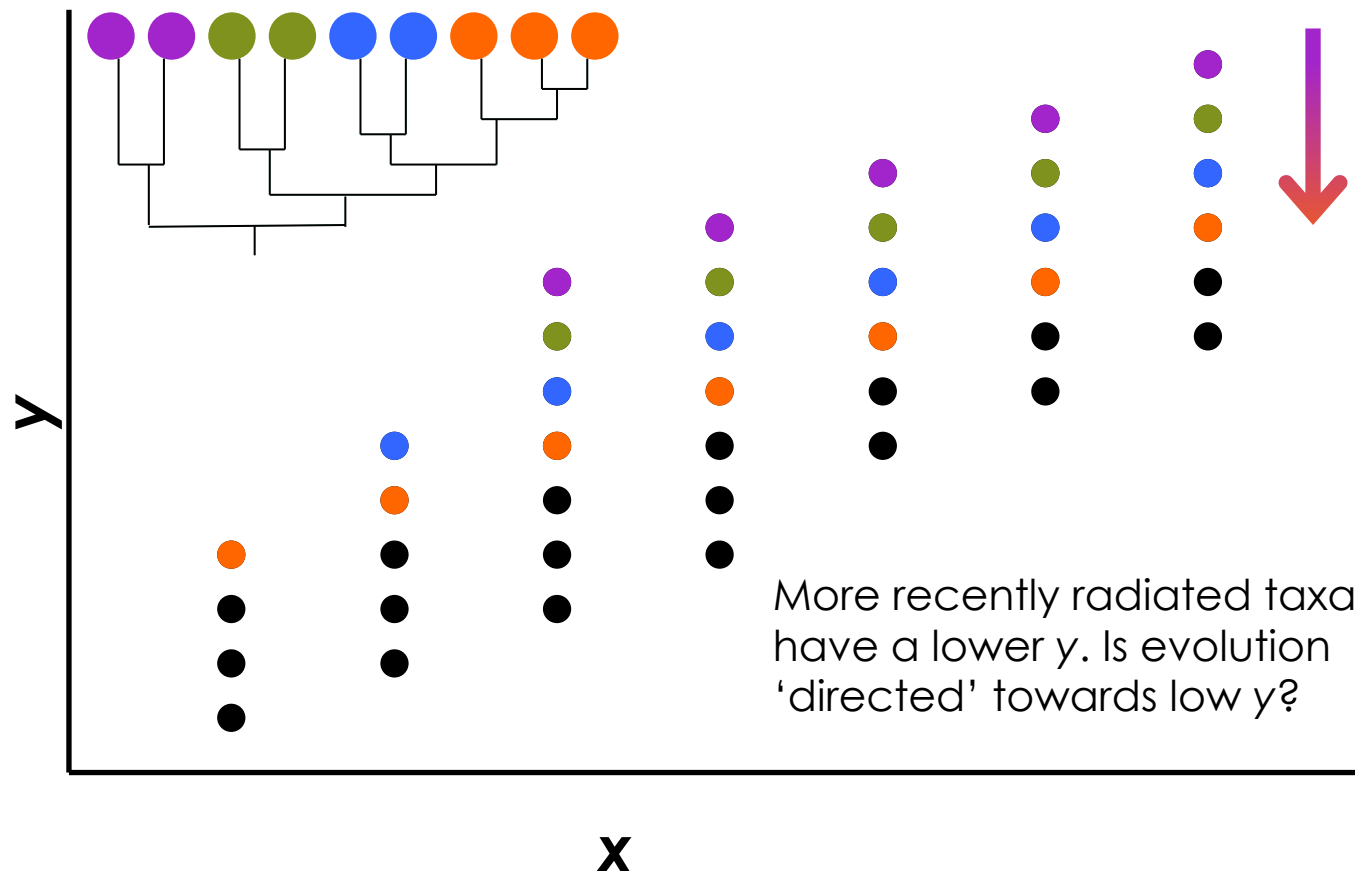
Are scaling relationships 'laws' around which adaptation works?





Interpreting patterns

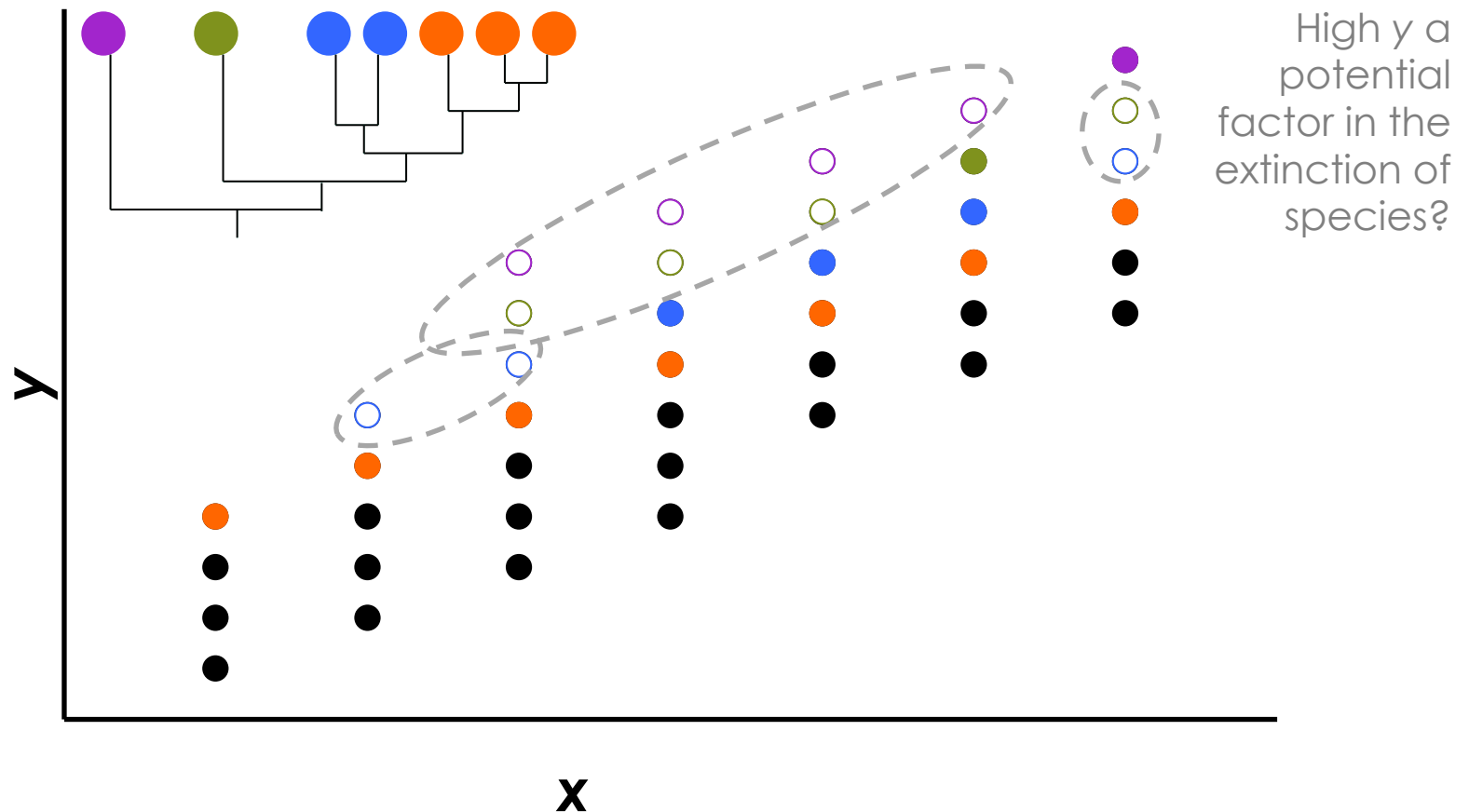
Is there a systematic phylogenetic structure in the dataset?





Interpreting patterns

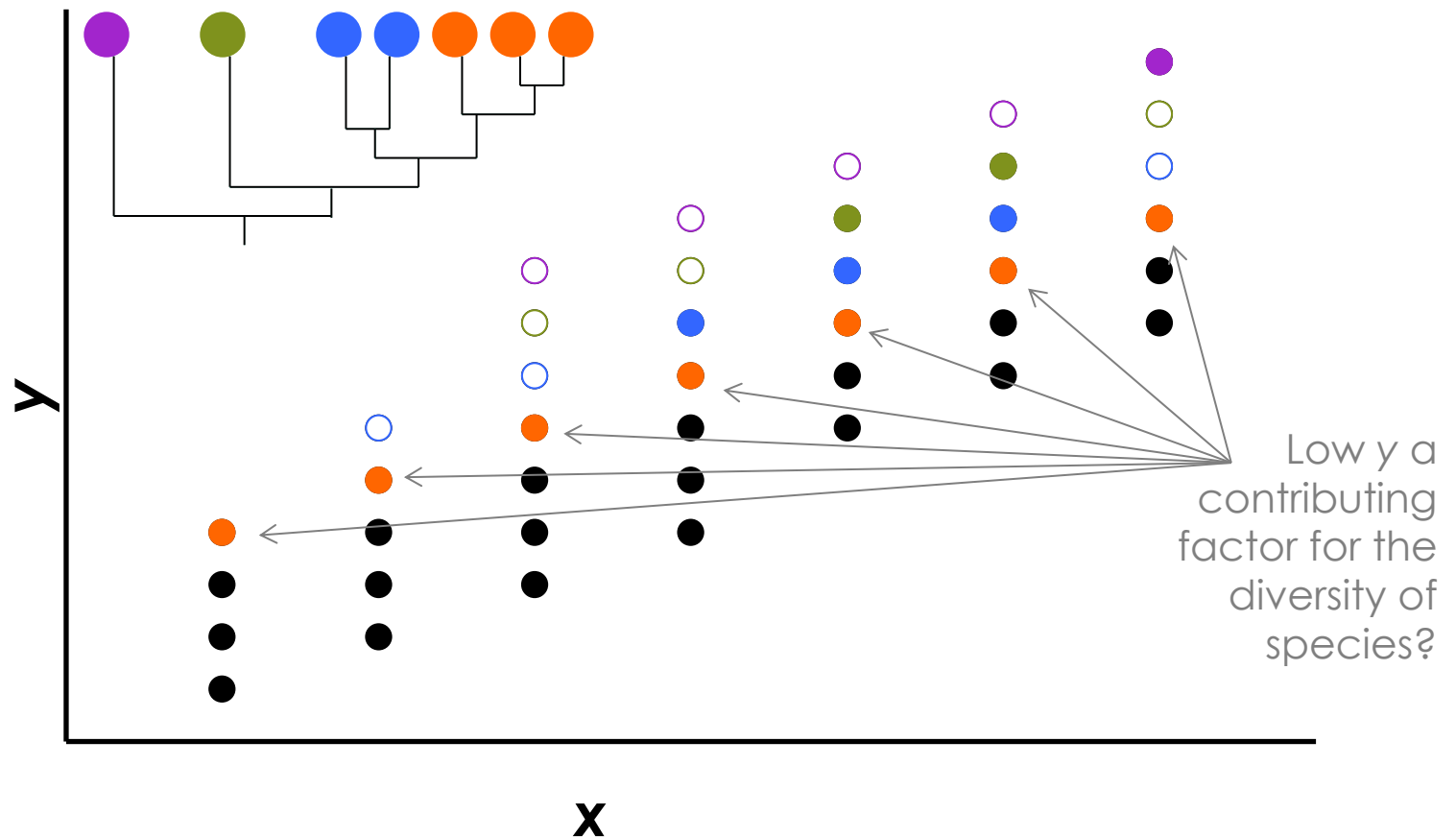
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Interpreting patterns

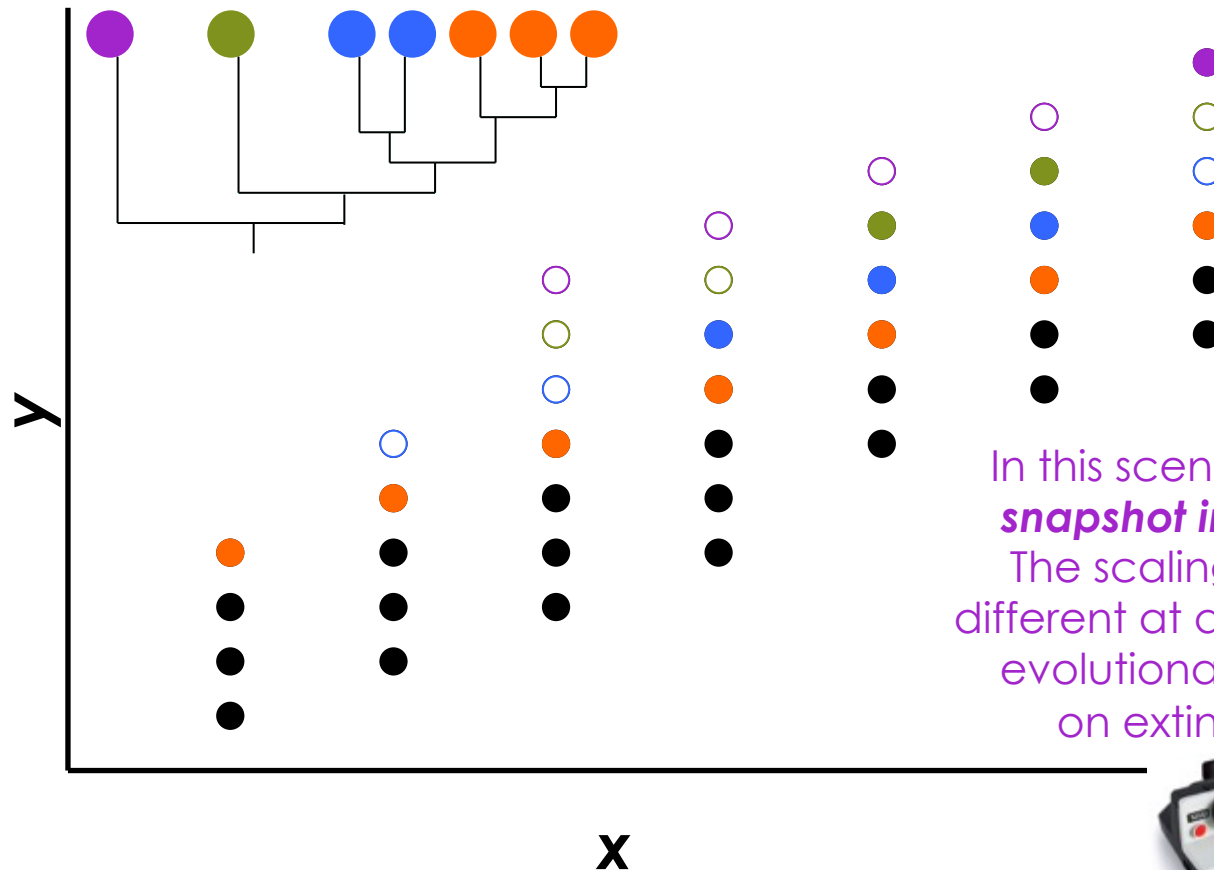
Is there a systematic phylogenetic structure in the dataset?





Interpreting patterns: snapshots

Is there a systematic phylogenetic structure in the dataset?

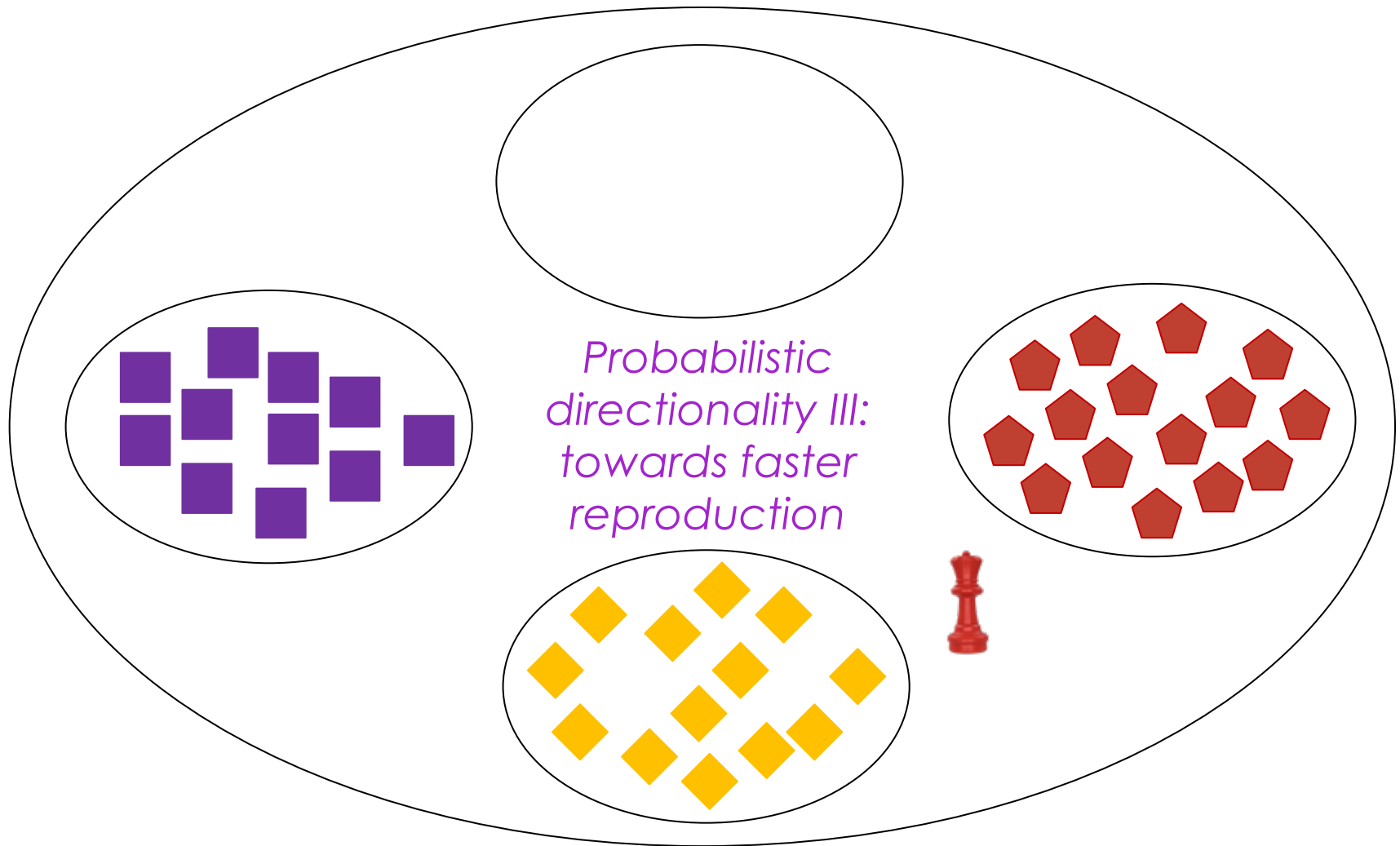


In this scenario, the scaling is a **snapshot in evolutionary time**. The scaling would have been different at different moments in evolutionary time (depending on extinction and radiation events)



A priori conditions and their consequences

Resources are finite.



Court Jester examples ?

'momentary solutions' ← → 'permanent solutions'



Within a niche, species are replaced ...
... by species with a more efficient
(i.e., faster at no additional cost)
reproduction.

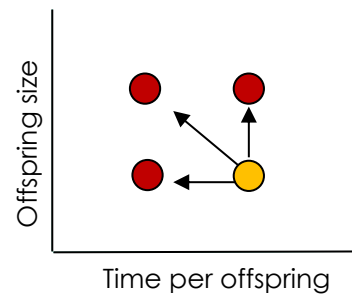
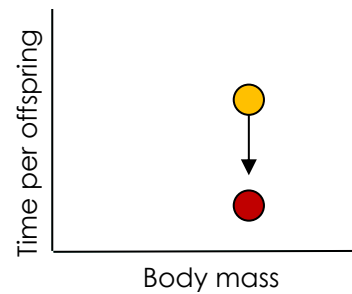
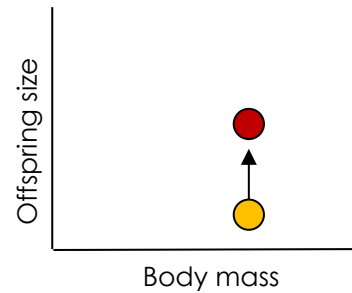
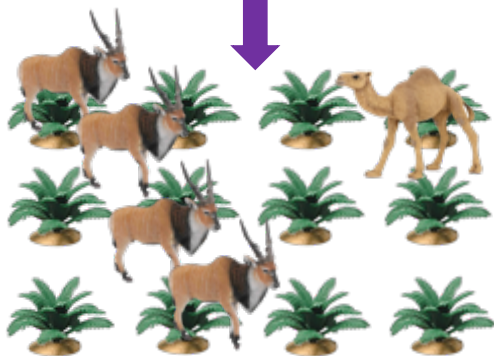


Stasis

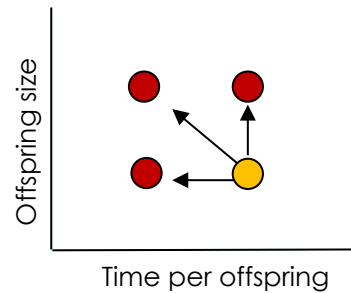
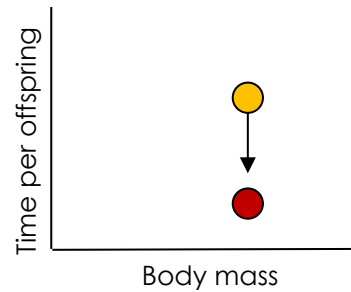
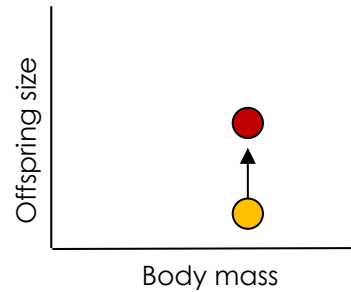
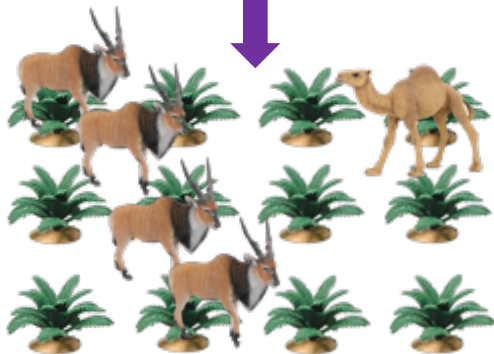




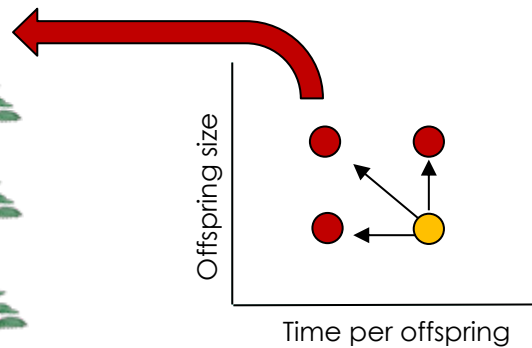
Competition for limited resources



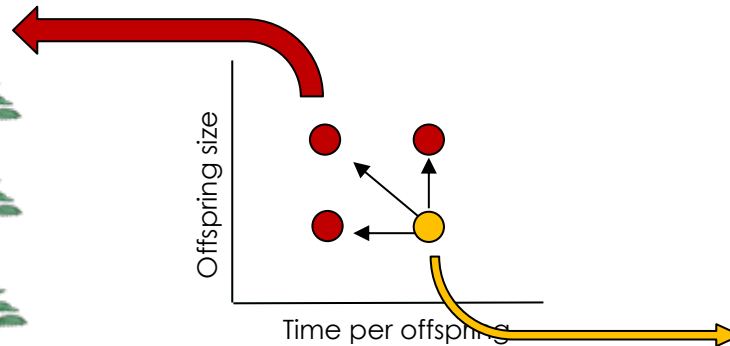
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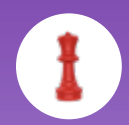


Competition for limited resources



Competition for limited resources

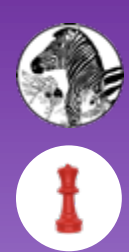




Darwinian evolution is a set of rules where the one constant (demographic) selective pressure is to outreproduce competitors.

*In the presence of competitors for limited resources, Darwinian selection should always go in the **direction** of a 'Darwinian Demon'.*

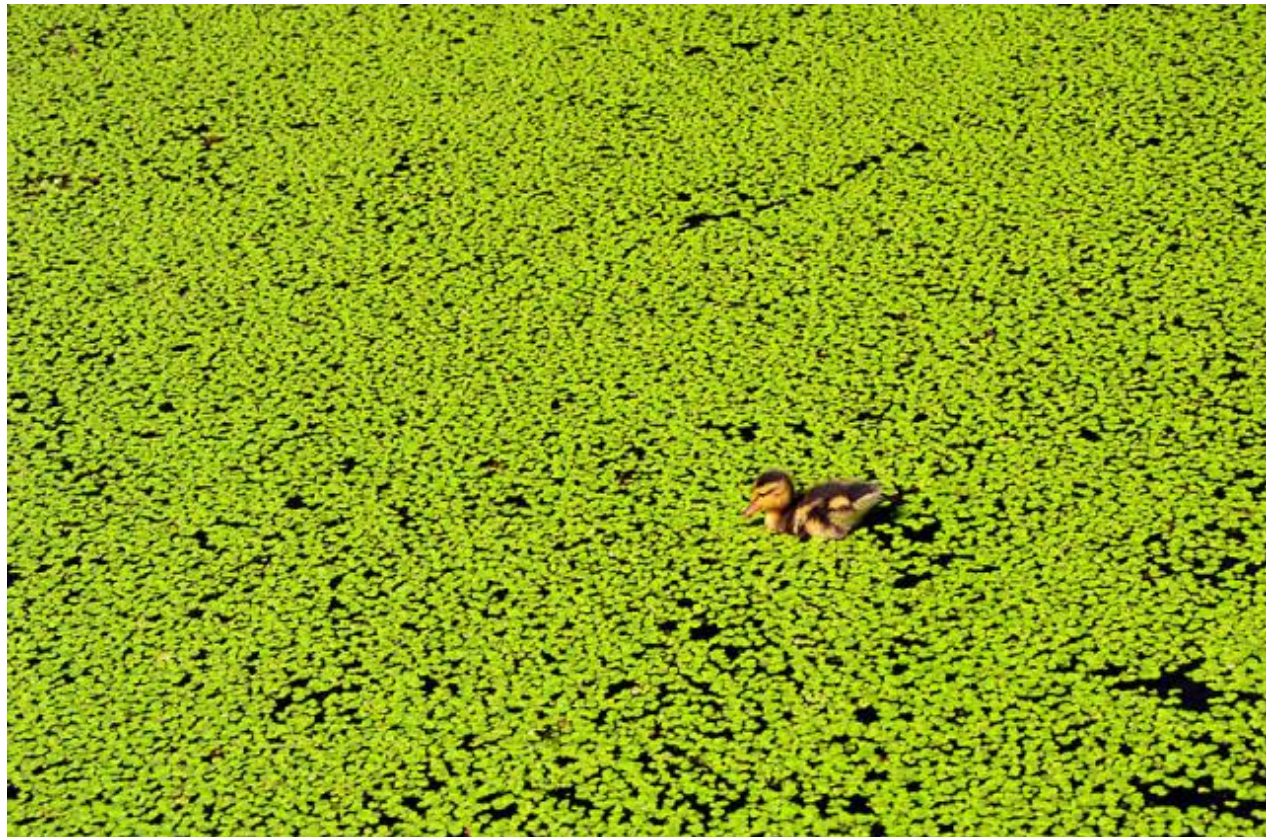




Darwinian demon



An organism that starts reproducing directly after birth, producing a large number of surviving offspring at extreme speed without ever dying.

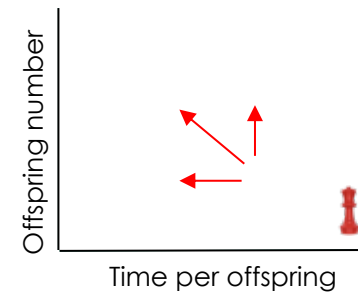
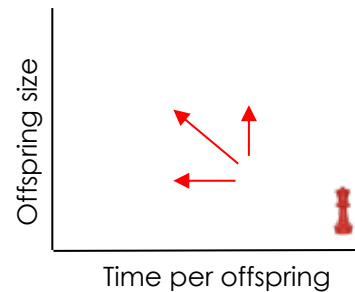
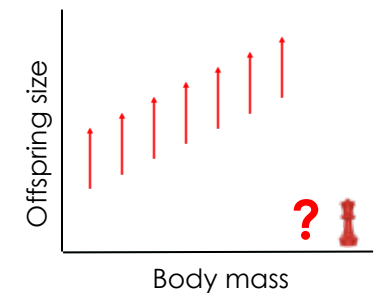
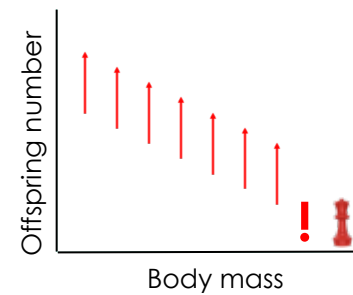
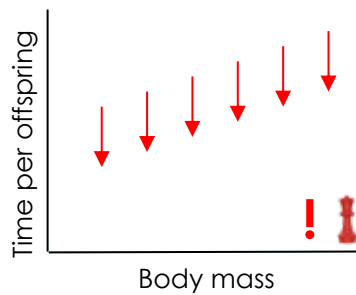




Darwinian demon



An organism that starts reproducing directly after birth, producing a large number of surviving offspring at extreme speed without ever dying.



FASTER





How do species achieve a faster reproduction?

We do not know (at least, in mammals).

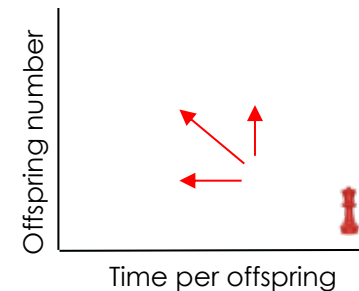
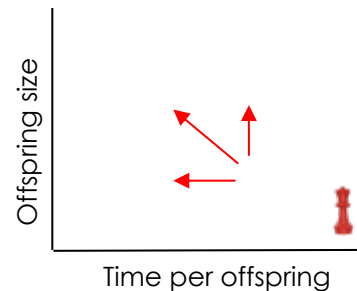


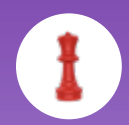
How do species achieve a faster reproduction?

We do not know (at least, in mammals).

How do we measure the speed of reproduction?

As 'Life History' ('pace of life').





Life history theory contradicts /
overlooks directional evolution.

Mammal life history

'fast'

Pace of Life

'slow'

High

Metabolism

Low

Short

Times

Long

(gestation, longevity, growth,
time to 1st reproduction)

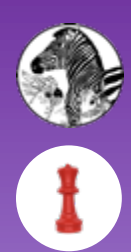
Many
Altricial

Offspring / time

Few
Precocial

same lifetime output





Mammal life history

'fast'

Pace of Life

'slow'

High

Metabolism

Low

Short

Times

Long

(gestation, longevity, growth,
time to 1st reproduction)

Many
Altricial

Offspring / time

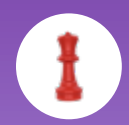
Few
Precocial

High

Mortality

Low





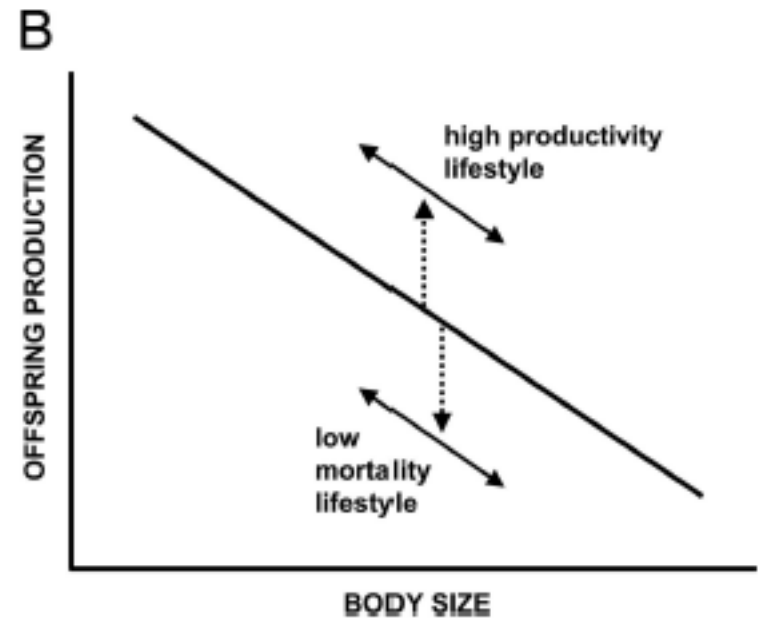
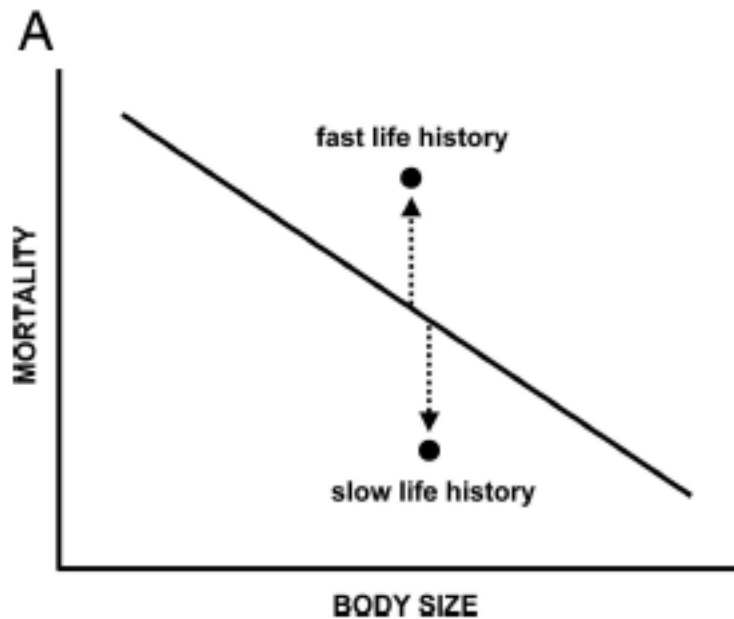
Evolution of
life history strategies is
understood as different solutions
to a tradeoff situation.

Life history scaling

A lifestyle view of life-history evolution

F. Stephen Dobson*

PNAS | November 6, 2007 | vol. 104 | no. 45 | 17565–17566



Effects of body size and lifestyle on evolution of mammal life histories

Richard M. Sibly^{*†‡} and James H. Brown^{‡§¶}

PNAS | November 6, 2007 | vol. 104 | no. 45 | 17707–17712

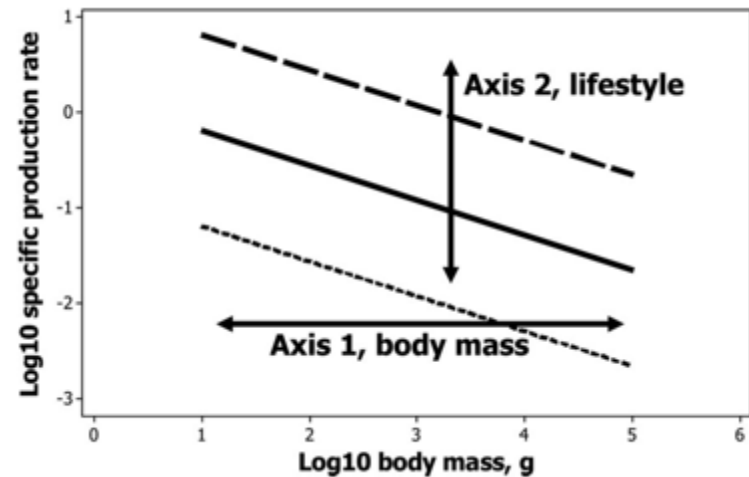
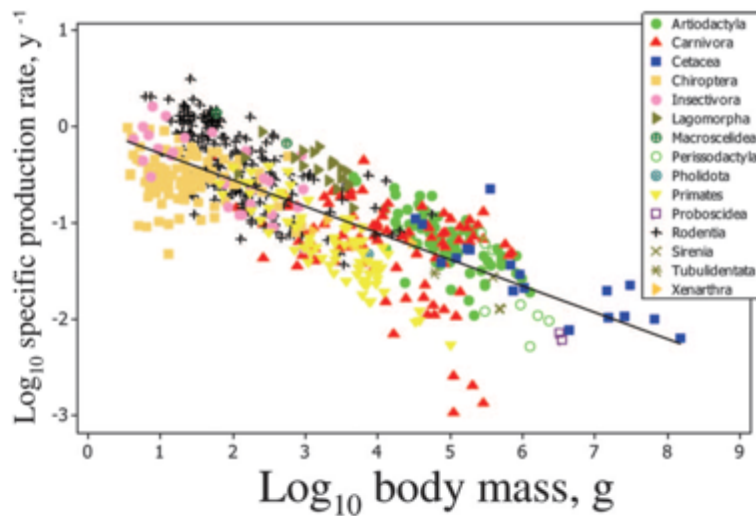
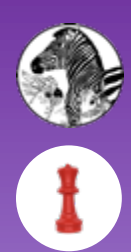


Fig. 4. The two major axes of the slow-fast life-history continuum, body mass, and lifestyle. To the well known axis of allometric variation due to body size, we have added a second orthogonal axis based on ecological lifestyle. Here the solid line represents an unspecialized ancestral condition, the dashed line depicts a more productive "live fast die young" lifestyle, and the dotted line shows a lifestyle with a lower death rate, slower life history, and consequently lower production.



The tradeoff fallacy

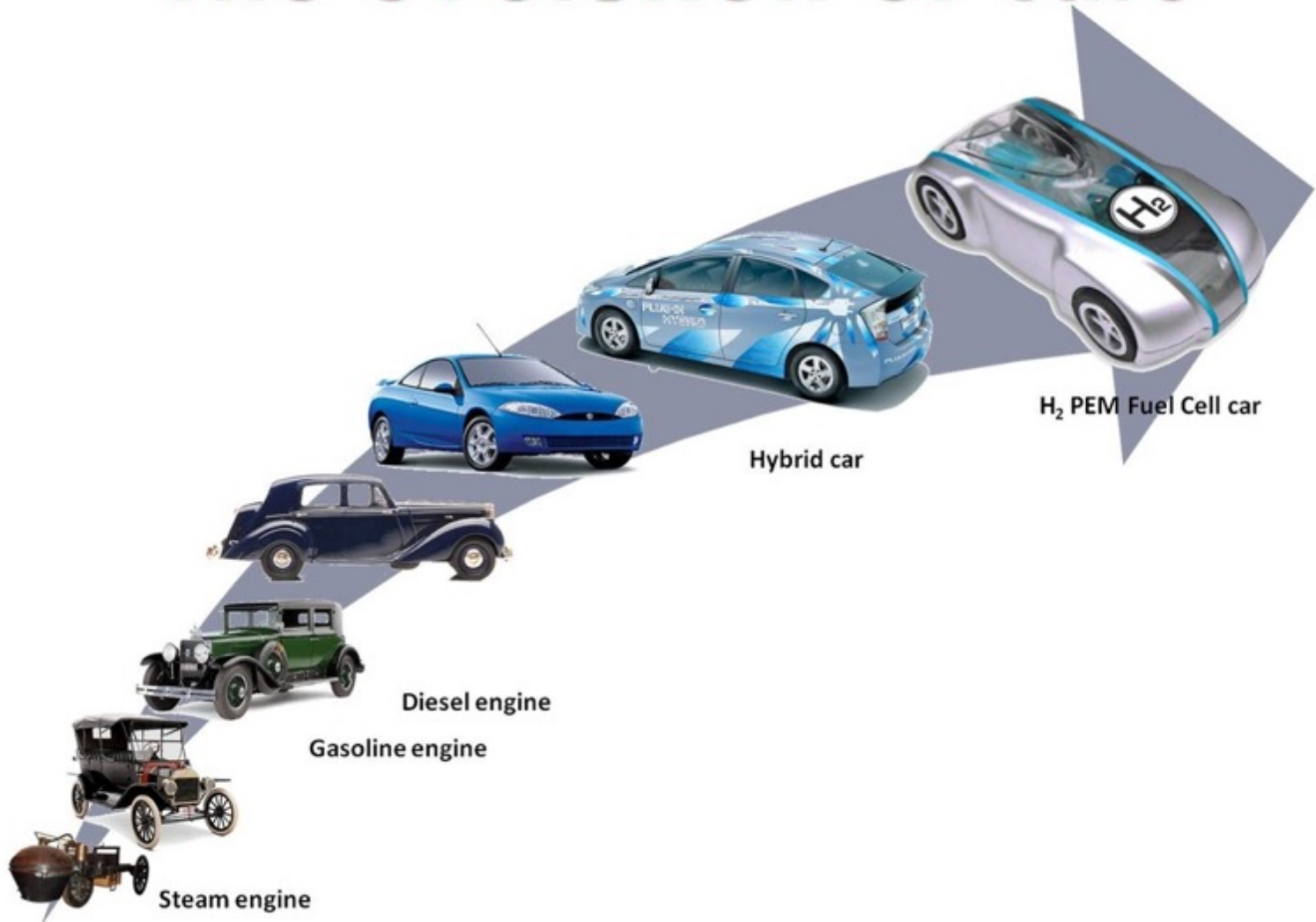
Saying that you either invest more into reproduction (live fast, produce many offspring at a time) or more into maintenance (live slower, produce less offspring at a time but over a longer period) ...

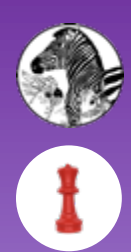
... is like saying that with a given amount of fuel, you either transport a certain load a certain distance, or a higher load a shorter distance

ignoring the possibility that someone might develop a more efficient engine.



The evolution of cars





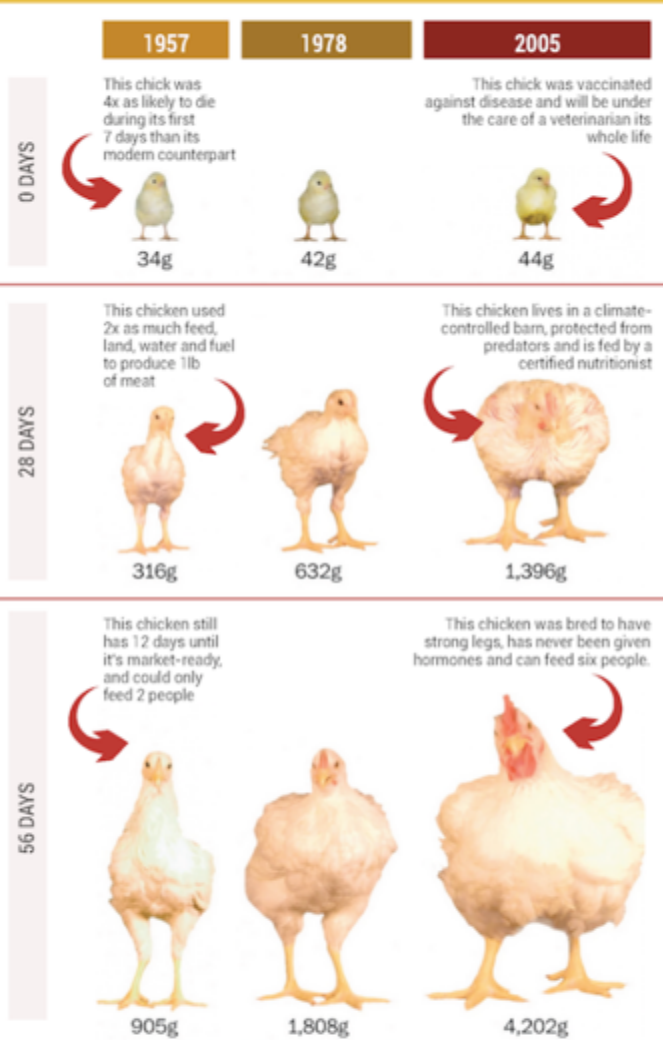
The tradeoff fallacy

Saying that you either invest more into reproduction (live fast, produce many offspring at a time) or more into maintenance (live slower, produce less offspring at a time but over a longer period) ...

... is like saying that if you want to have more meat on your chicken, you have to feed it more food for a longer period of time

ignoring the possibility that someone might breed an animal that grows faster on less food.

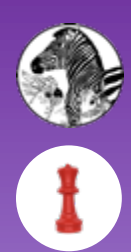
YEP, CHICKENS ARE BIGGER TODAY



It's no secret that today's chickens are bigger than in years past. They're also the healthiest they've ever been. Find out how at chickencheck.in



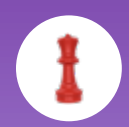
Note: 1,000 grams equals 2.2 pounds
Source: University of Alabama Meat Control
Image Credit: <https://www.washingtonpost.com/news/energy-environment/wp/2015/07/04/the-unbelievable-growth-of-american-food-factories-and-what-it-means/>




The tradeoff fallacy

Saying that you either invest more into reproduction (live fast, produce many offspring at a time) or more into maintenance (live slower, produce less offspring at a time but over a longer period) ...

... is ignoring the possibility that individuals (and taxa) might evolve that achieve a higher reproductive output with the same level of resources due to a higher efficiency.



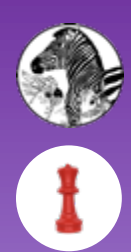
High reproductive effort is associated with decreasing mortality late in life in captive ruffed lemurs

Morgane Tidière¹  | Jean-François Lemaître¹ | Guillaume Douay² |

Mylisa Whipple³ | Jean-Michel Gaillard¹

Am J Primatol. 2017;**79**:e22677.

These findings indicate that individual quality rather than trade-off drives the association between reproductive success and survival pattern.

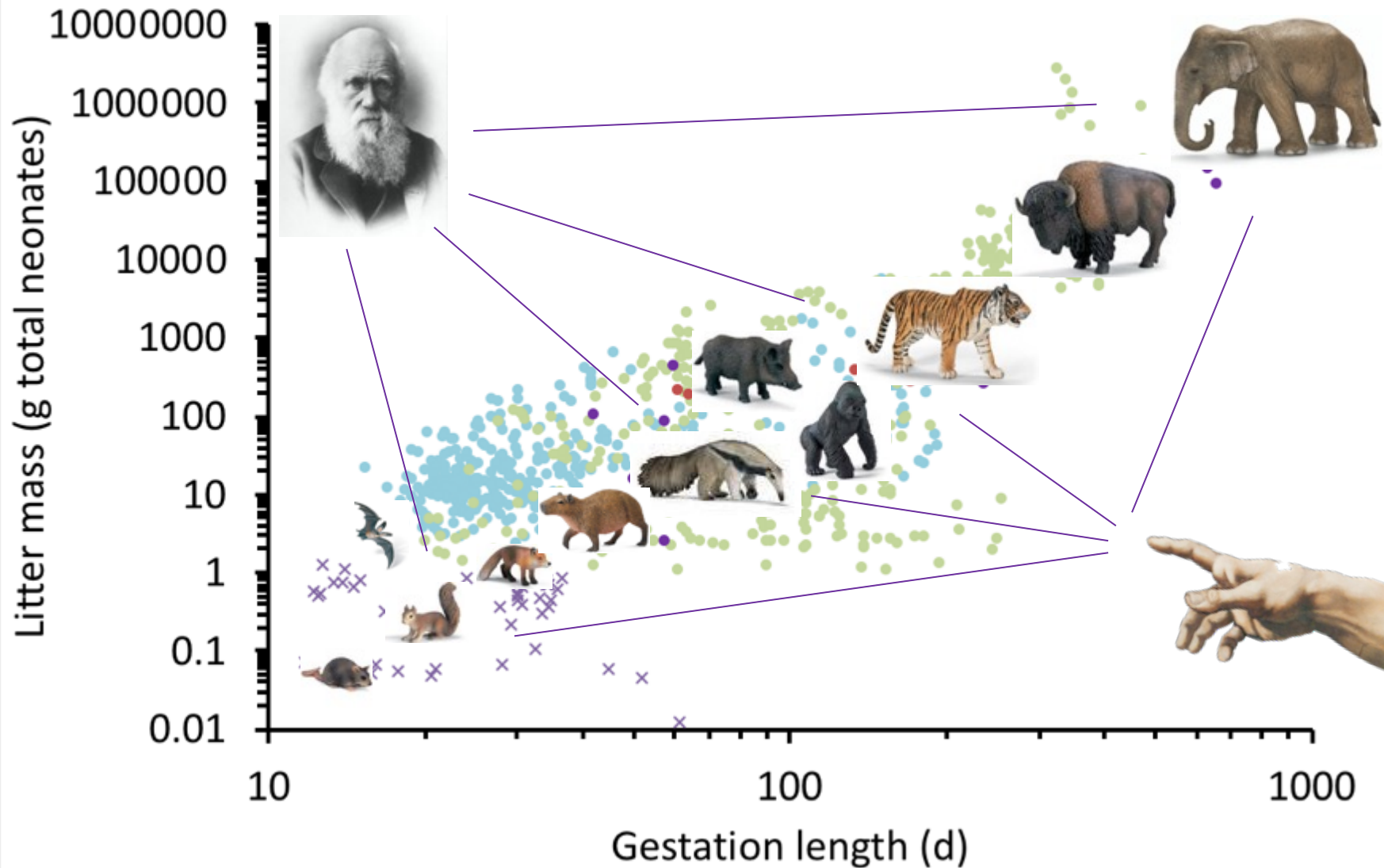


The tradeoff fallacy

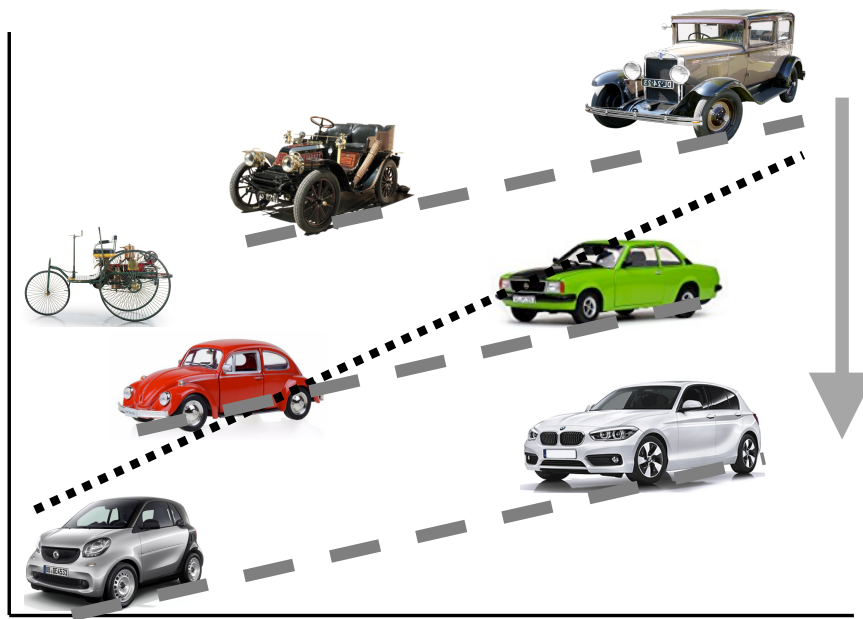
Saying that you either invest more into reproduction (live fast, produce many offspring at a time) or more into maintenance (live slower, produce less offspring at a time but over a longer period) ...

... is like saying you do not believe that evolution can find new solutions.

Two ways of being a creationist



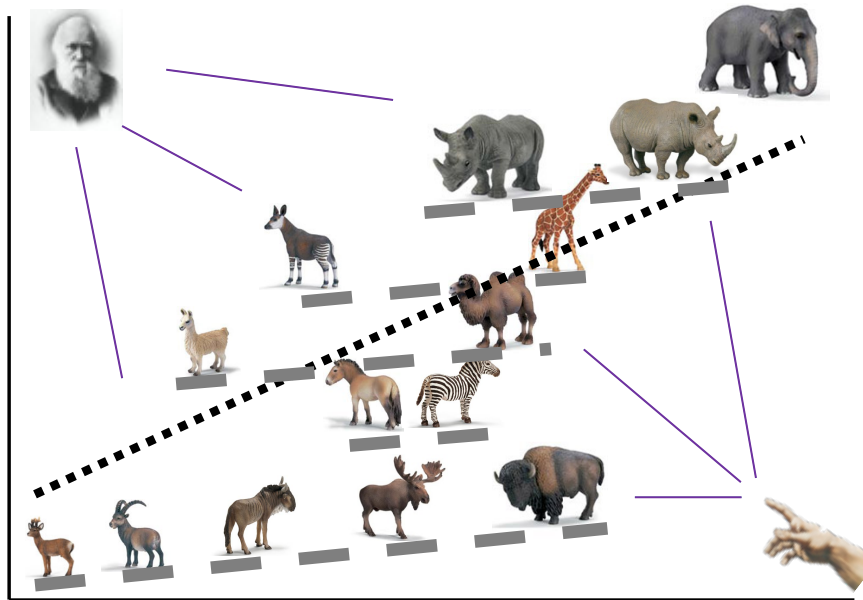
Energy per km



You would not consider the overall pattern a fixed law, but consider it with respect to technical progress.

Mass

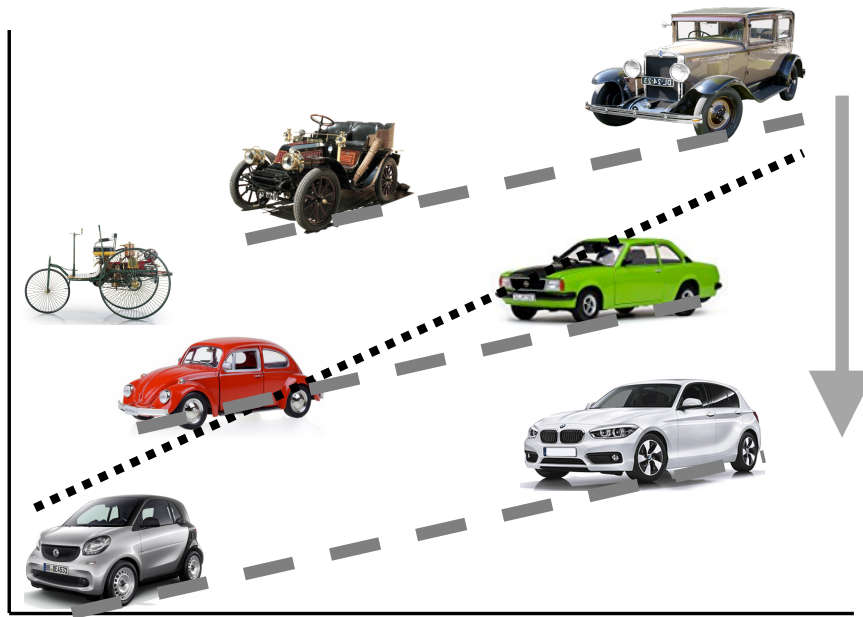
Time per offspring



Why would you consider this a pattern due to fixed life history tradeoff laws?

Mass

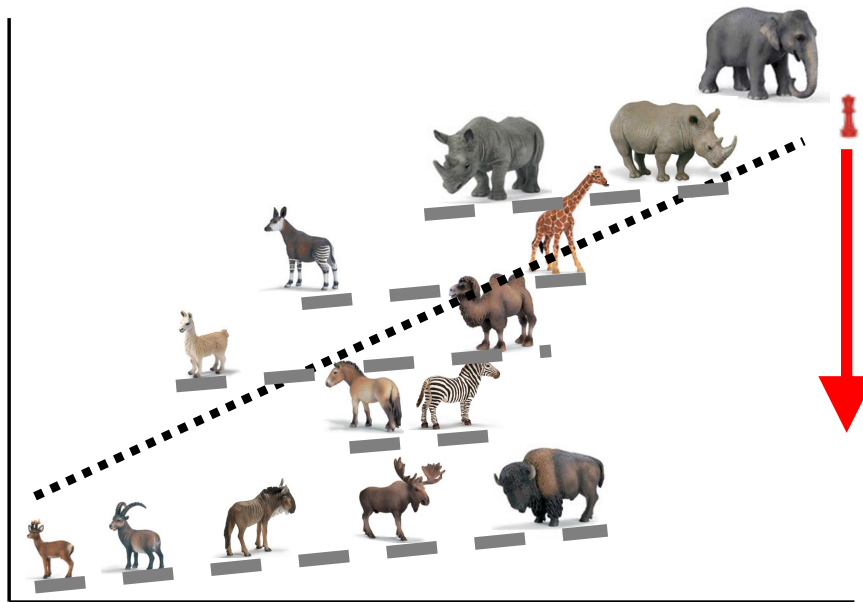
Energy per km



Mass

You would not consider the overall pattern a fixed law, but consider it with respect to technical progress.

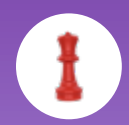
Time per offspring



Mass

Why would you consider this a pattern due to fixed life history tradeoff laws, and not rather a **snapshot** in a process of optimization?





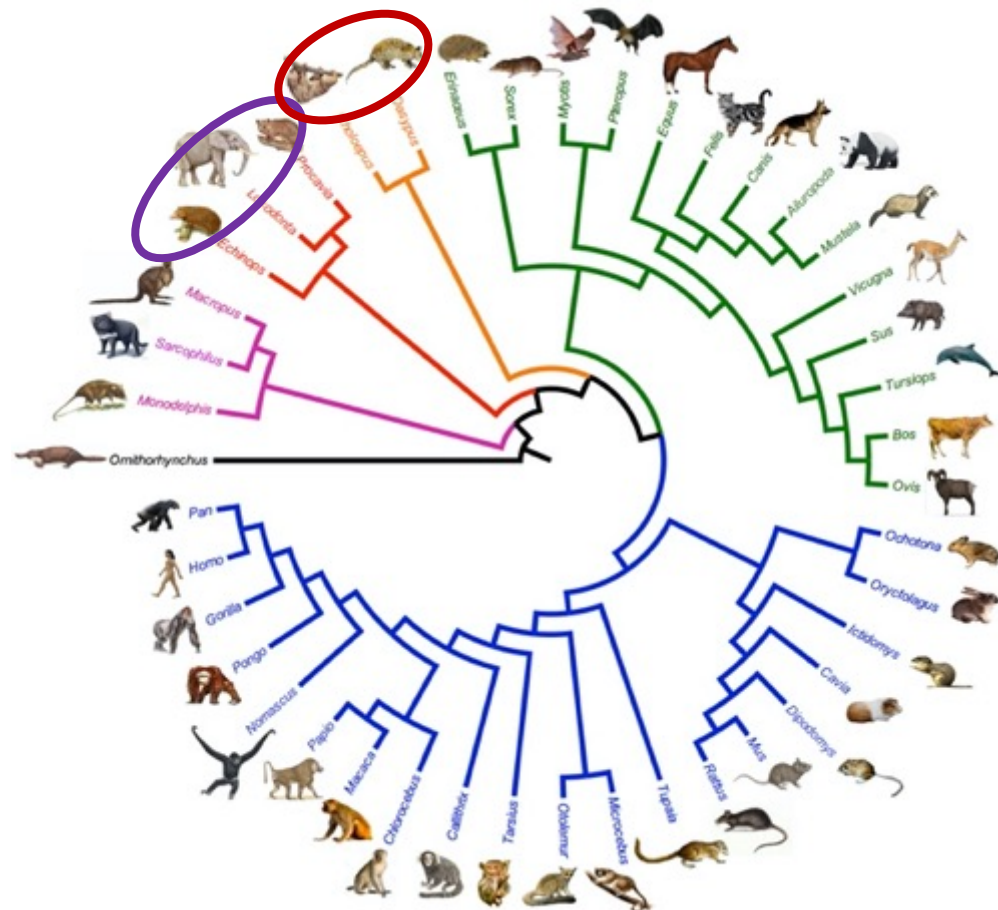
Assessing 'direction' / *Red Queen* / escalation / progress in life history

using the PanTheria dataset
(Jones et al. 2009)

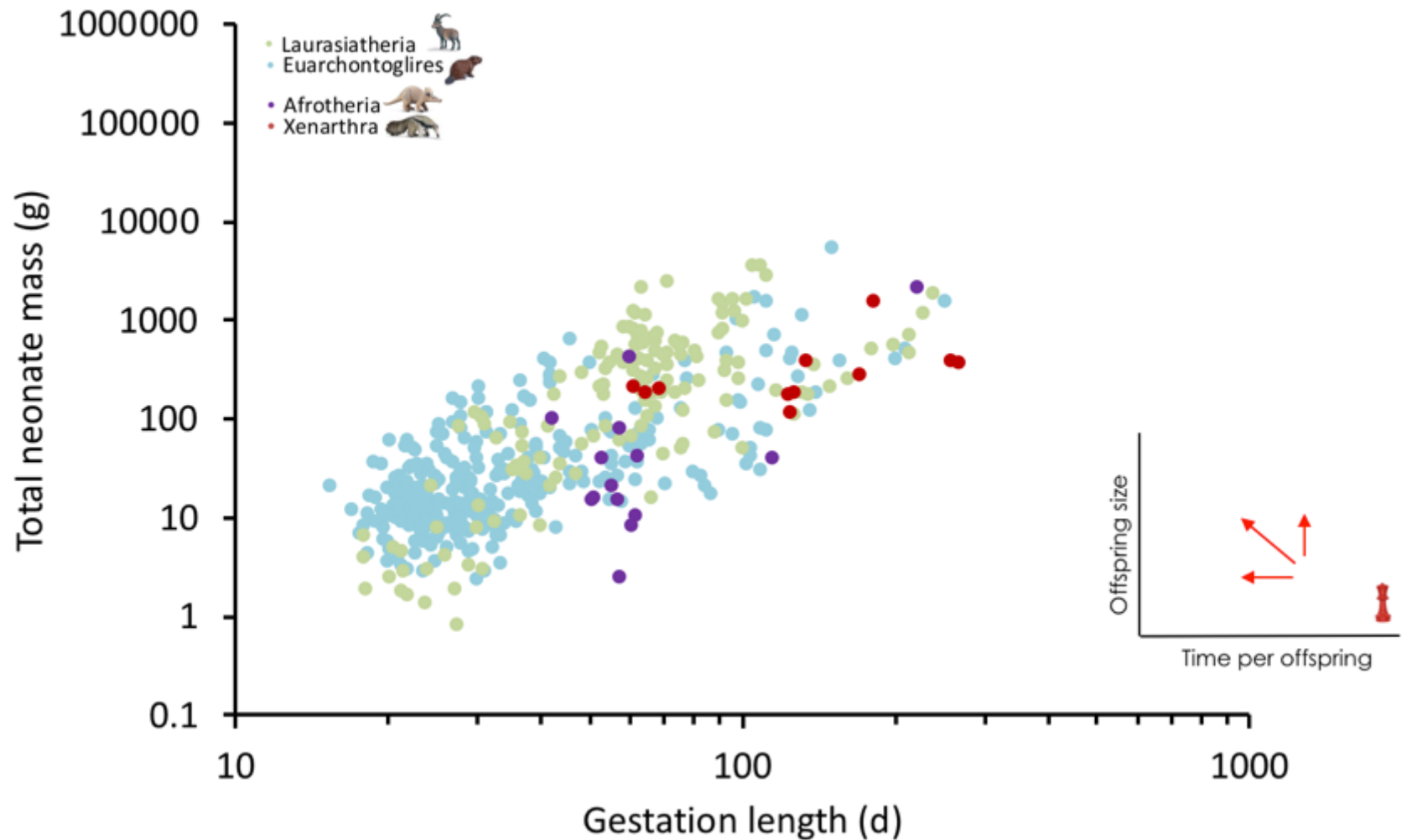


Eutherian superorder assessment

The eutherian superorders of Afrotheria and Xenarthra are not particularly speciose and could serve as a test case for clades that produced low extant diversity.

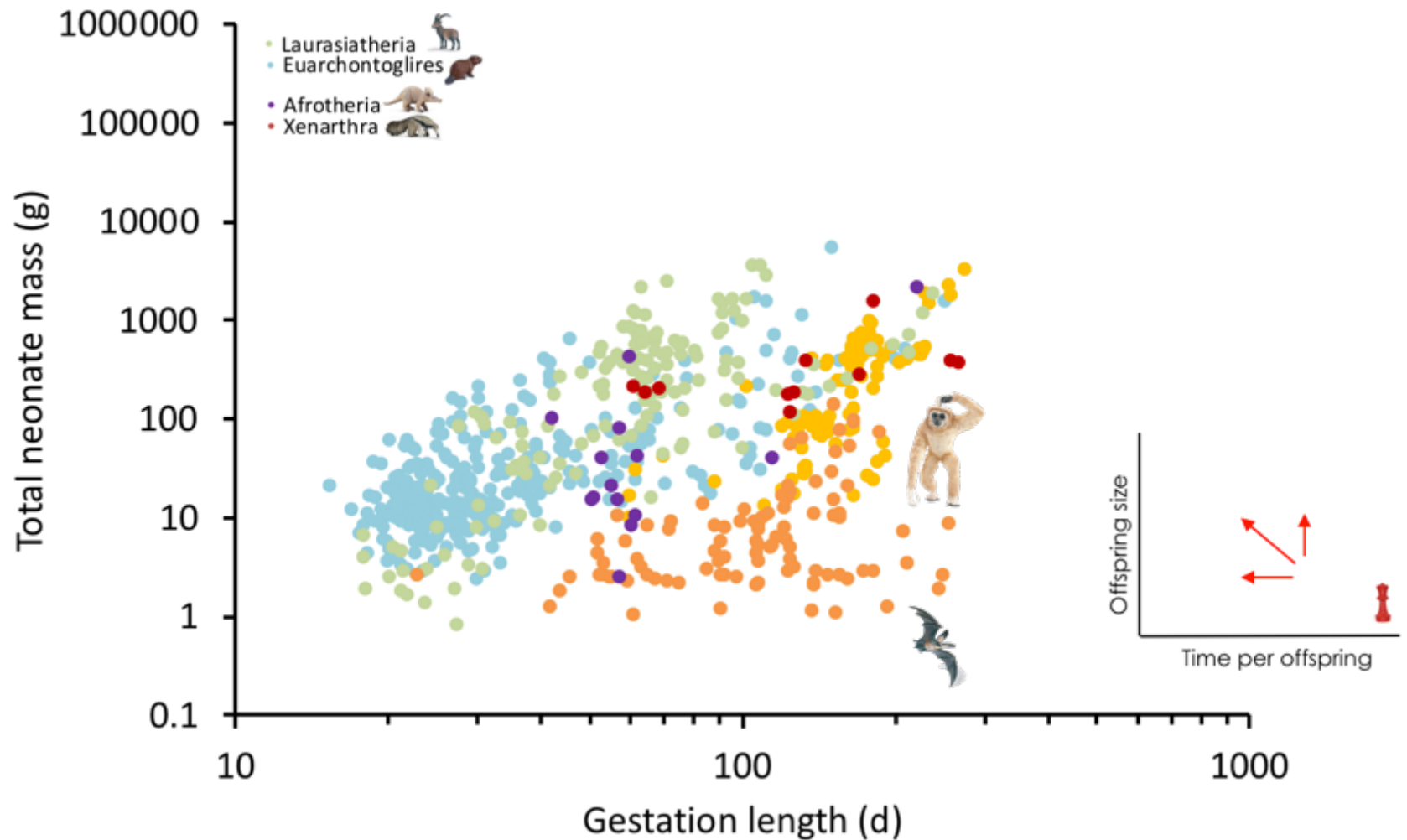


A clear picture for intrauterine growth?



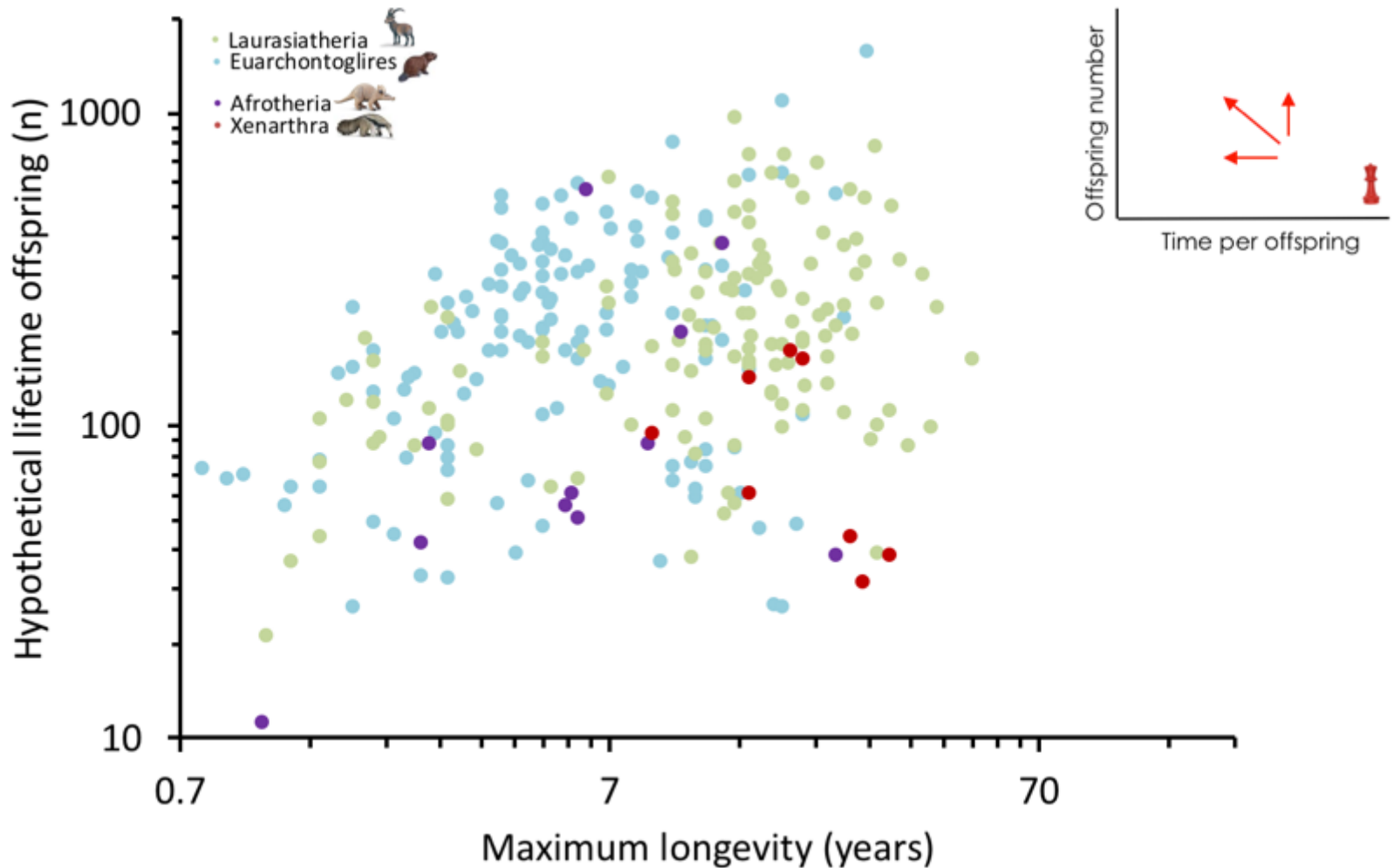
terrestrial, no primates/bats, no large herbivores

A clear picture for intrauterine growth?



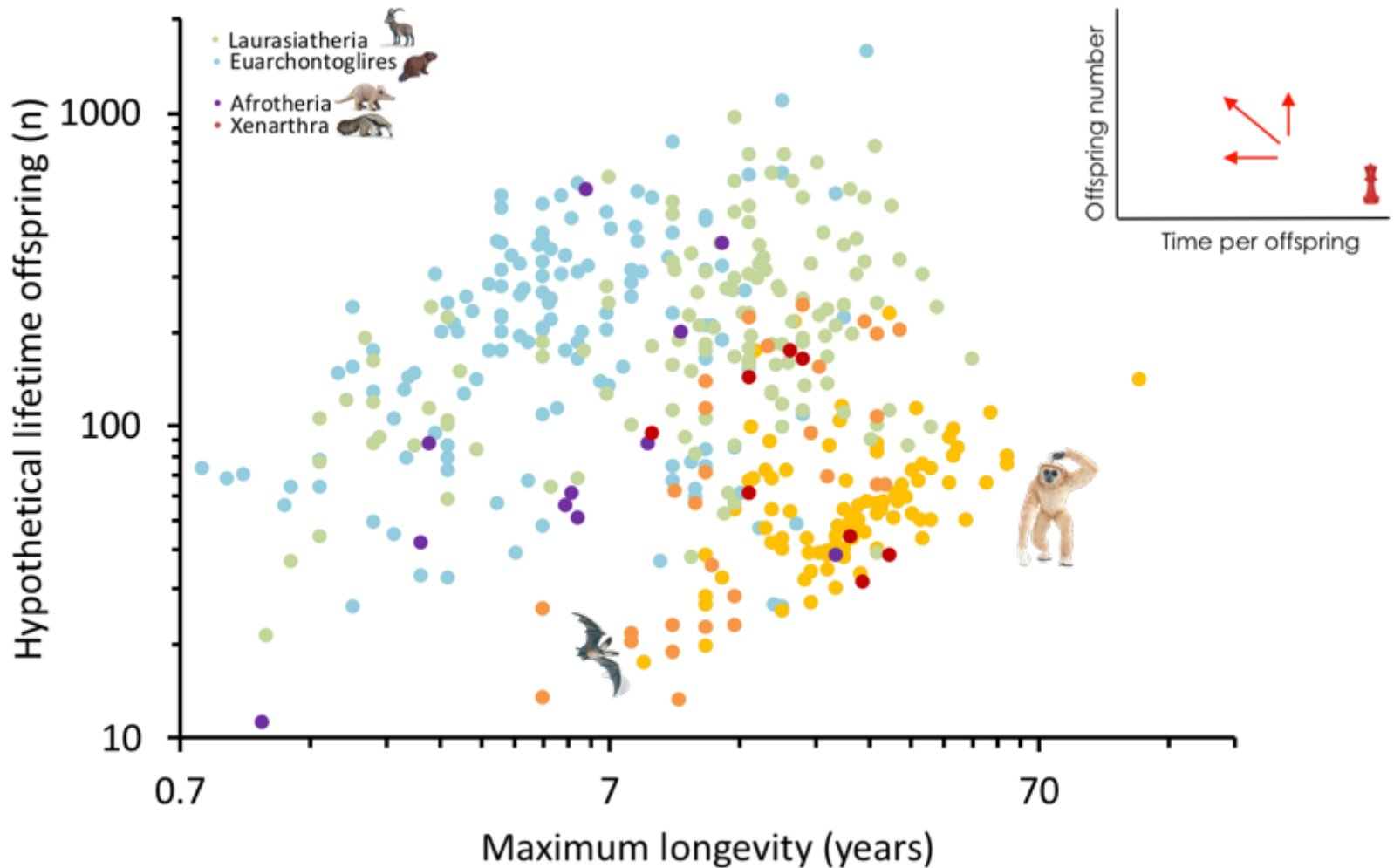
terrestrial, no large herbivores

A clear picture for lifetime offspring output?

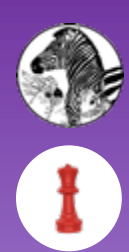


terrestrial, no bats/primates, no large herbivores

A clear picture for lifetime offspring output?



terrestrial, no large herbivores



Niche-specific assessment

Because niche space is less diverse at larger body sizes, large herbivores may be a particularly fruitful area of research for 'directed evolution'.



Herbivore
basic™



Herbivore
2.0™



Herbivore
professional™



Herbivore
ultimate™

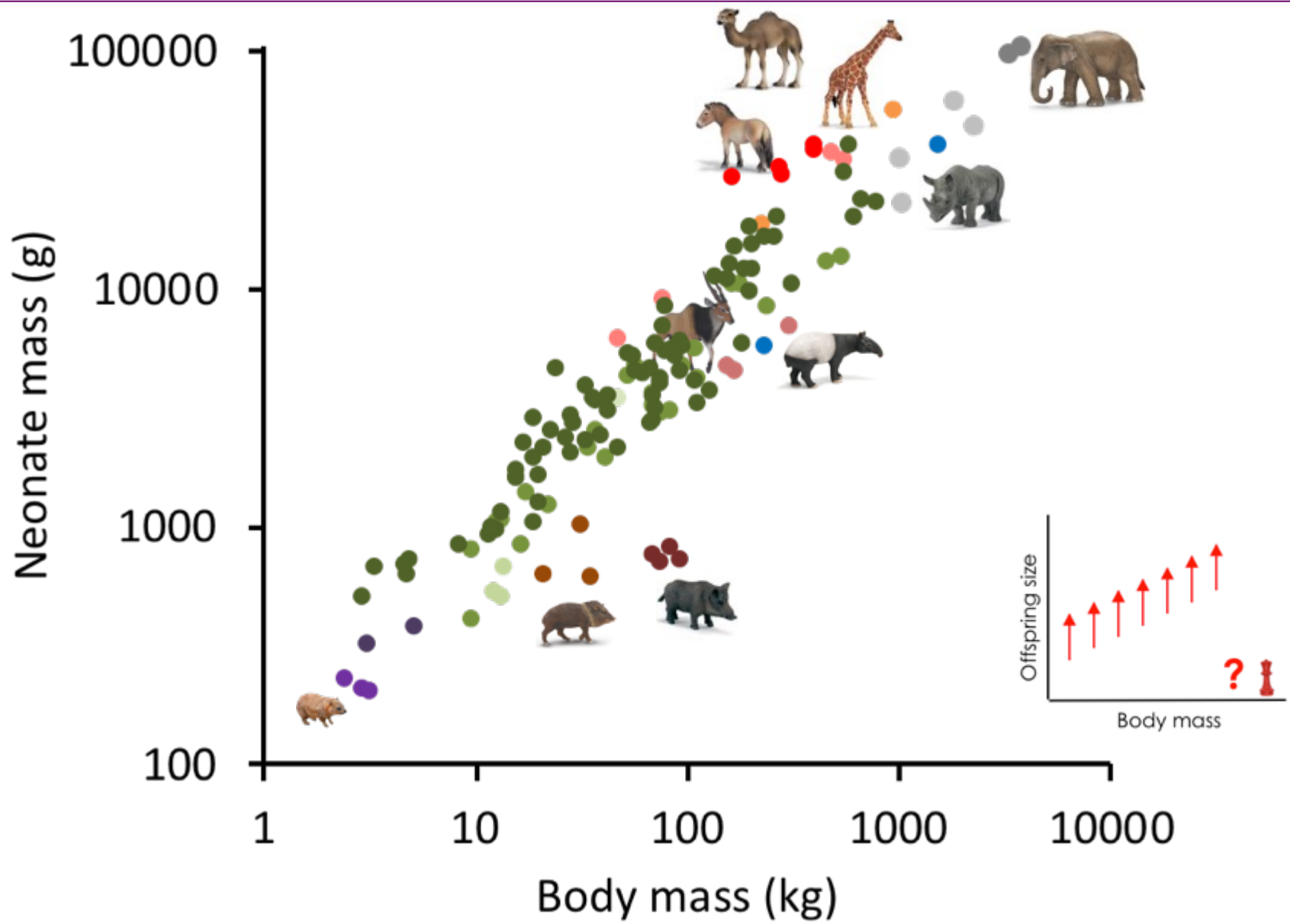


Niche-specific assessment

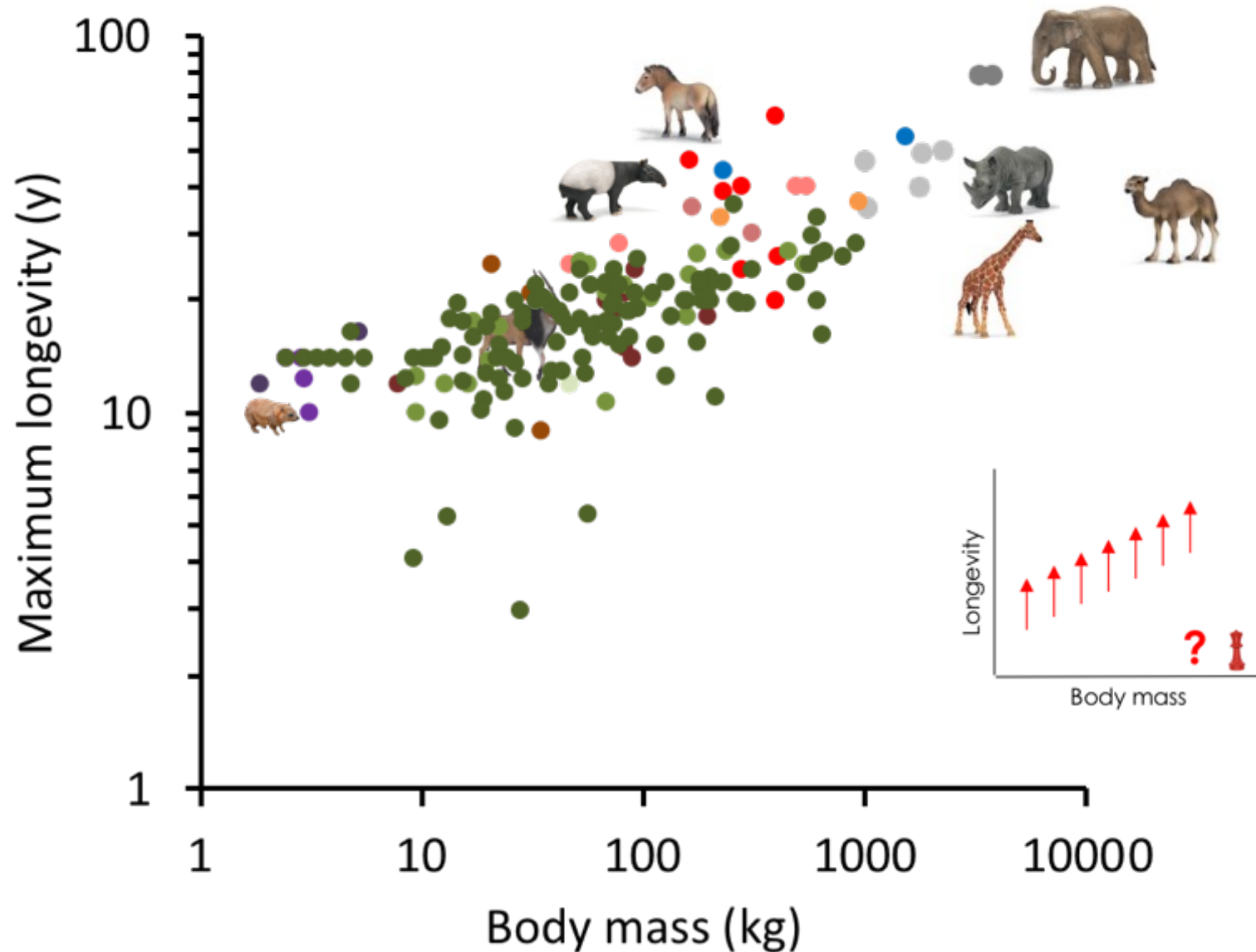
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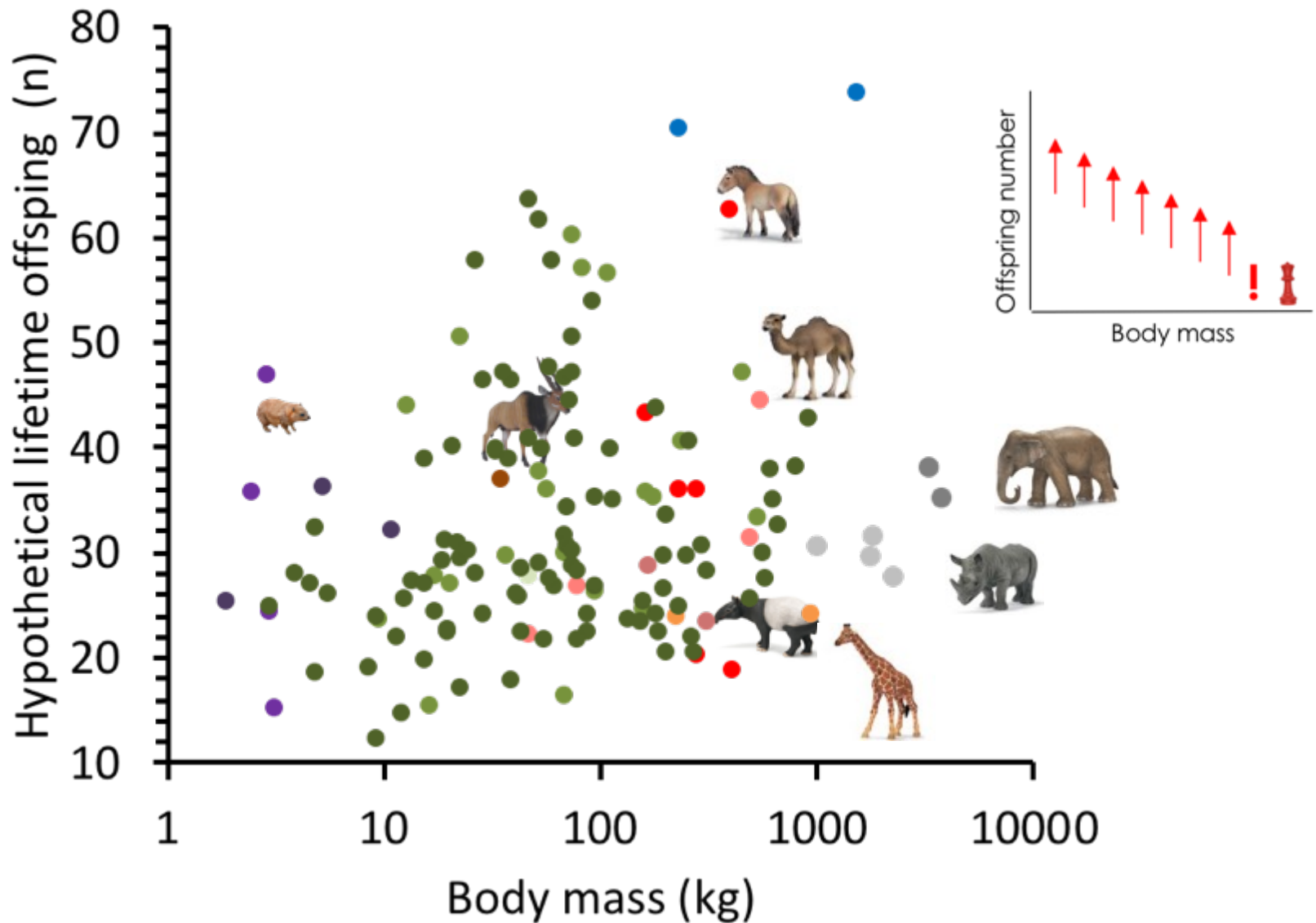
No clear picture for neonate mass



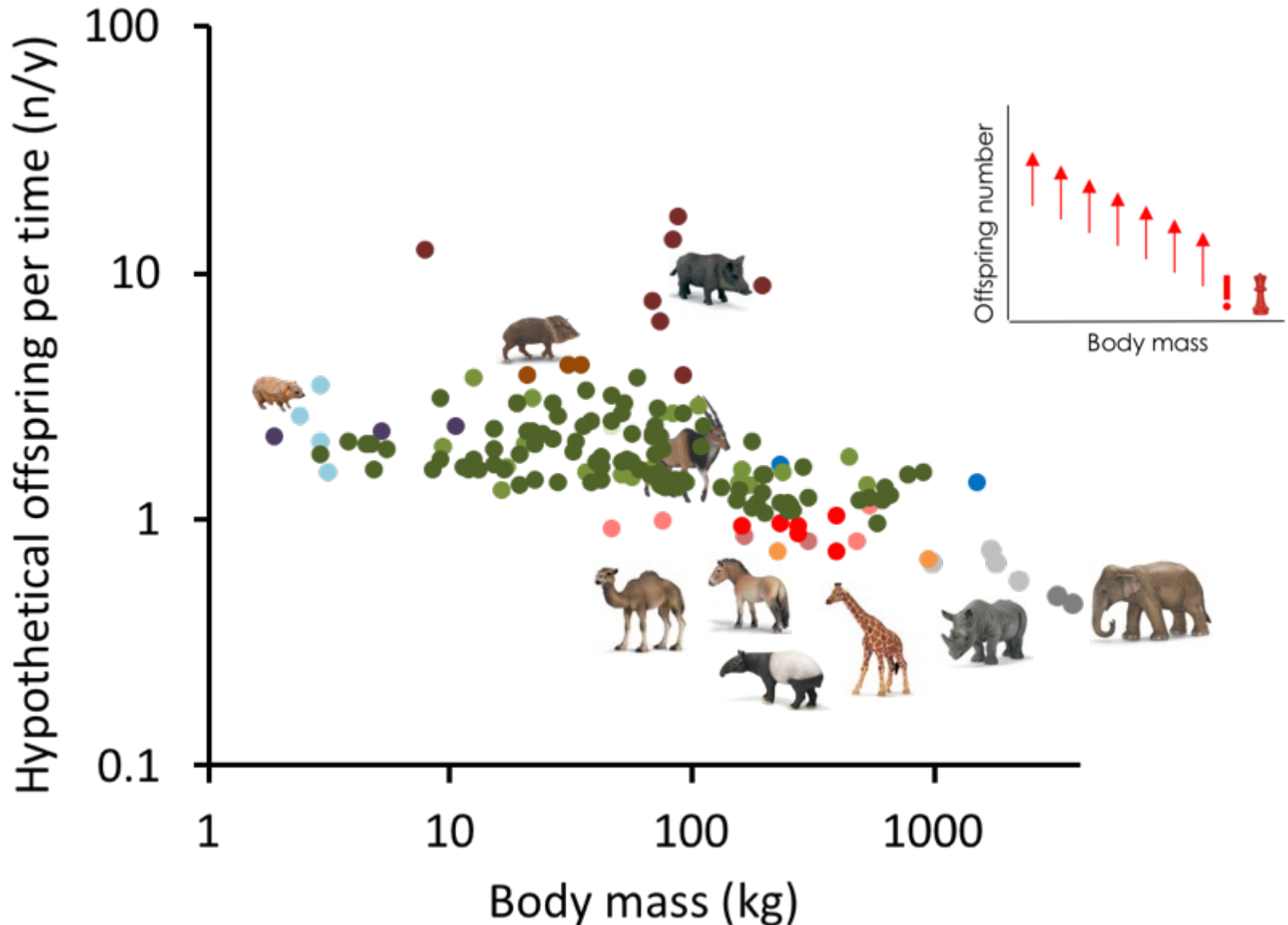
No clear picture for longevity



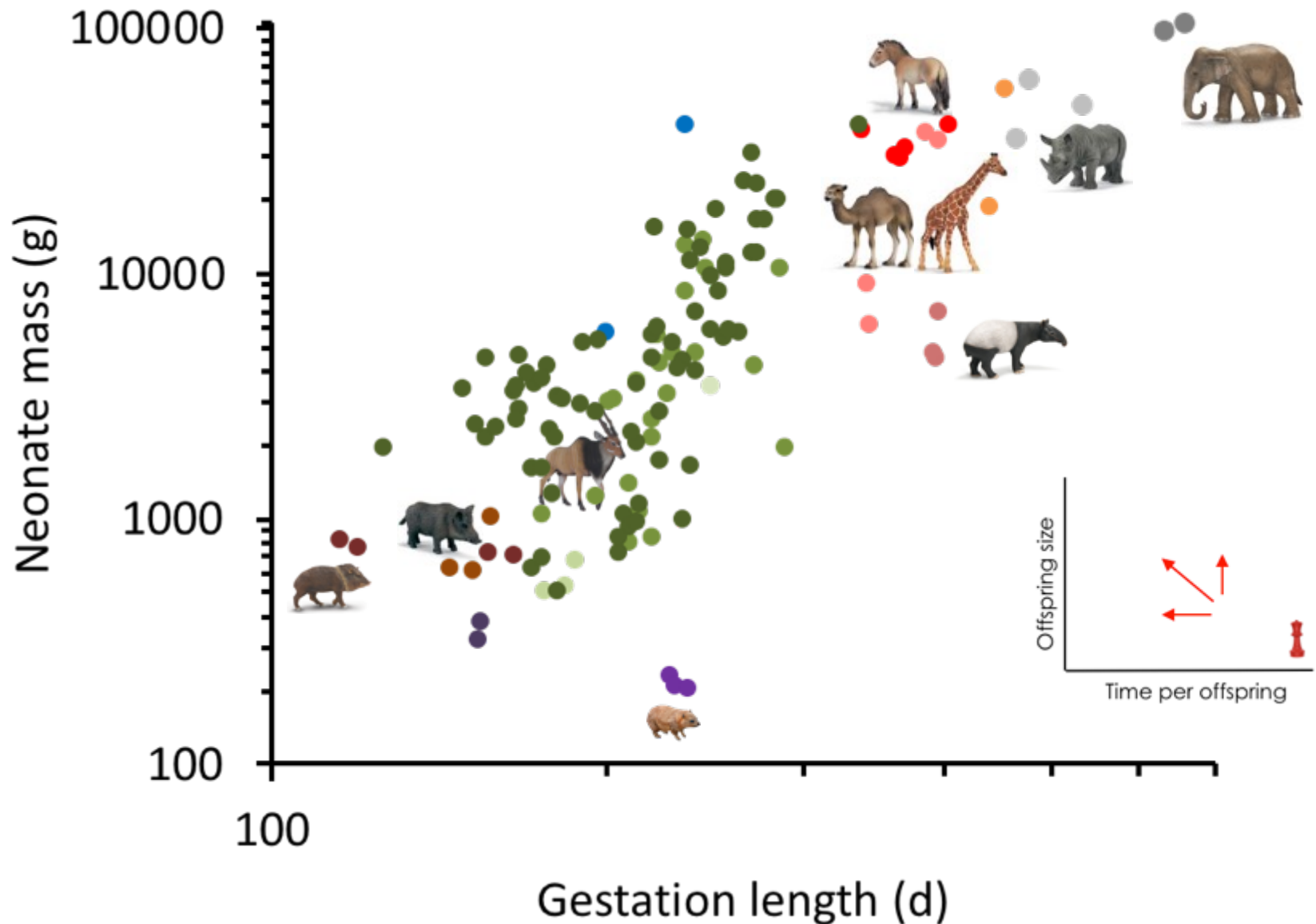
No effect for lifetime offspring



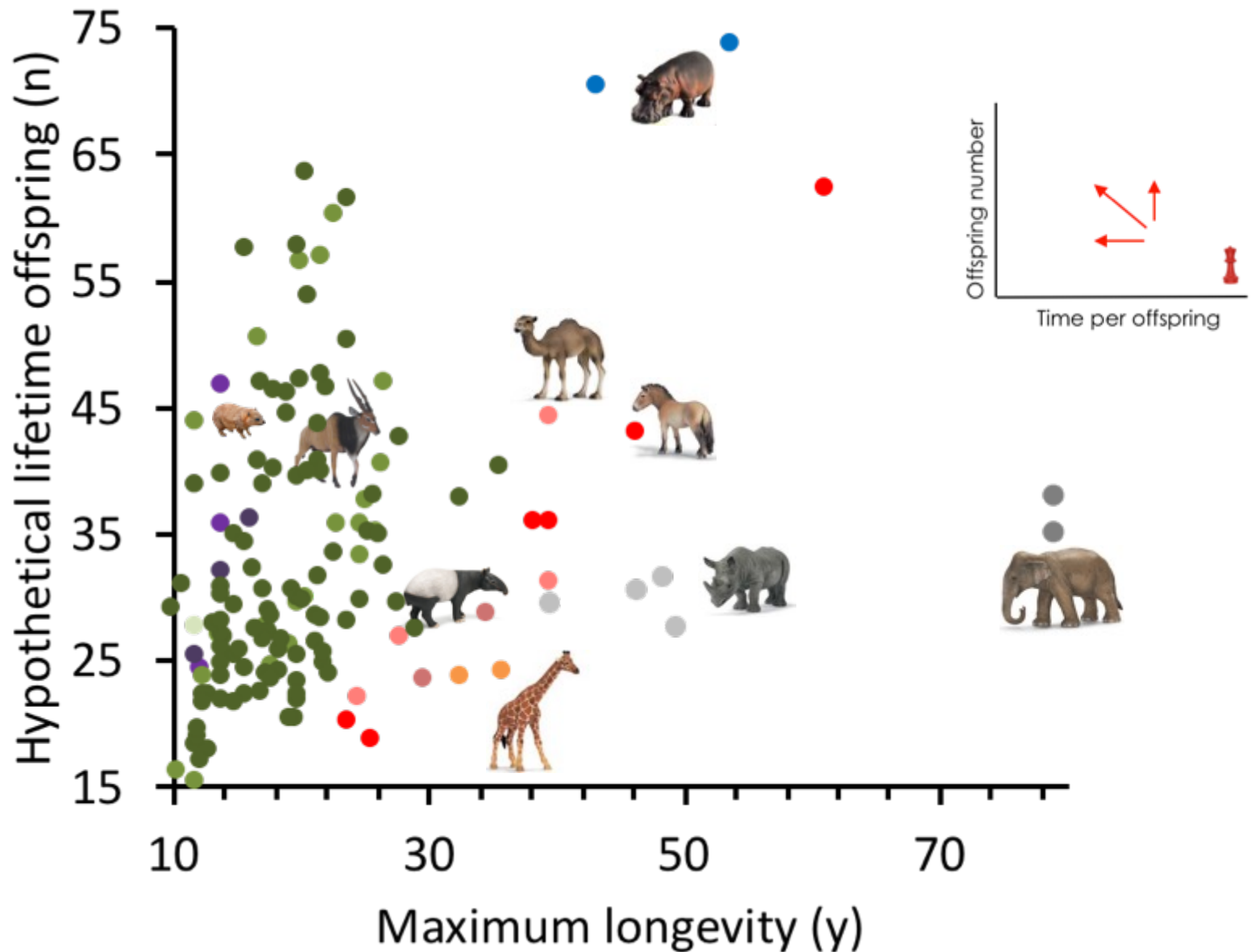
Clear effect for yearly offspring



A clear picture for intrauterine growth



A clear picture for lifetime offspring production





Summary, Conclusions & Outlook

Rather than understanding tradeoffs along the fast-slow continuum as fixed physical laws, they can be considered as representing the efficiency of the organisms from which the data was taken – and that efficiency may evolve.

Within the boundaries of a specific niche, species possibly compete by demographic means: by evolving a faster reproduction.

Life history characteristics appear to be linked to taxonomic groups.





The interesting question ...

... what allowed the remaining extant species of the 'slower' taxa to survive?





Summary, Conclusions & Outlook

Rather than understanding tradeoffs along the fast-slow continuum as fixed physical laws, they can be considered as representing the efficiency of the organisms from which the data was taken – and that efficiency may evolve.

Within the boundaries of a specific niche, species possibly compete by demographic means: by evolving a faster reproduction.

Life history characteristics appear to be linked to taxonomic groups.

We would predict that during geological history, 'faster' species were not replaced by 'slower' species.

The physiological means by which species differ in their life history are not well explored.



By what means do cattle achieve faster intrauterine growth than horses?



Gestation periods

Cattle	280 days
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Horse	340 days
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Dromedary	390 days
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Okapi	440 days
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Hyrax	230 days
-------	----------

Hare	42 days
------	---------

Elephant	22 months
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Blue whale	12 months
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thank you for your attention

