How large should whales be?

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Southern Right whale | photo credit Brian Skerry

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How Large Should Whales Be?

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Abstract

The evolution and distribution of species body sizes for terrestrial mammals is well-explained by a macroevolutionary tradeoff between short-term selective advantages and long-term extinction risks from increased species body size, unfolding above the 2 *g* minimum size induced by thermoregulation in air. Here, we consider whether this same tradeoff, formalized as a constrained convection-reaction-diffusion system, can also explain the sizes of fully aquatic mammals, which have not previously been considered. By replacing the terrestrial minimum with a pelagic one, at roughly 7000 *g*, the terrestrial mammal tradeoff model accurately predicts, with no tunable parameters, the observed body masses of all extant cetacean species, including the 175,000,000 *g* Blue Whale. This strong agreement between theory and data suggests that a universal macroevolutionary tradeoff governs body size evolution for all mammals, regardless of their habitat. The dramatic sizes of cetaceans can thus be attributed mainly to the increased convective heat loss is water, which shifts the species size distribution upward and pushes its right tail into ranges inaccessible to terrestrial mammals. Under this macroevolutionary tradeoff, the largest expected species occurs where the rate at which smaller-bodied species move up into large-bodied niches approximately equals the rate at which extinction removes them.

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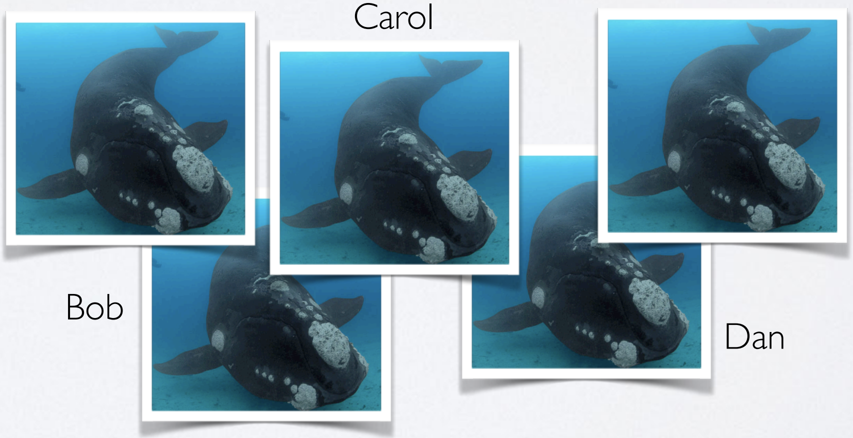
Microevolution

below species level

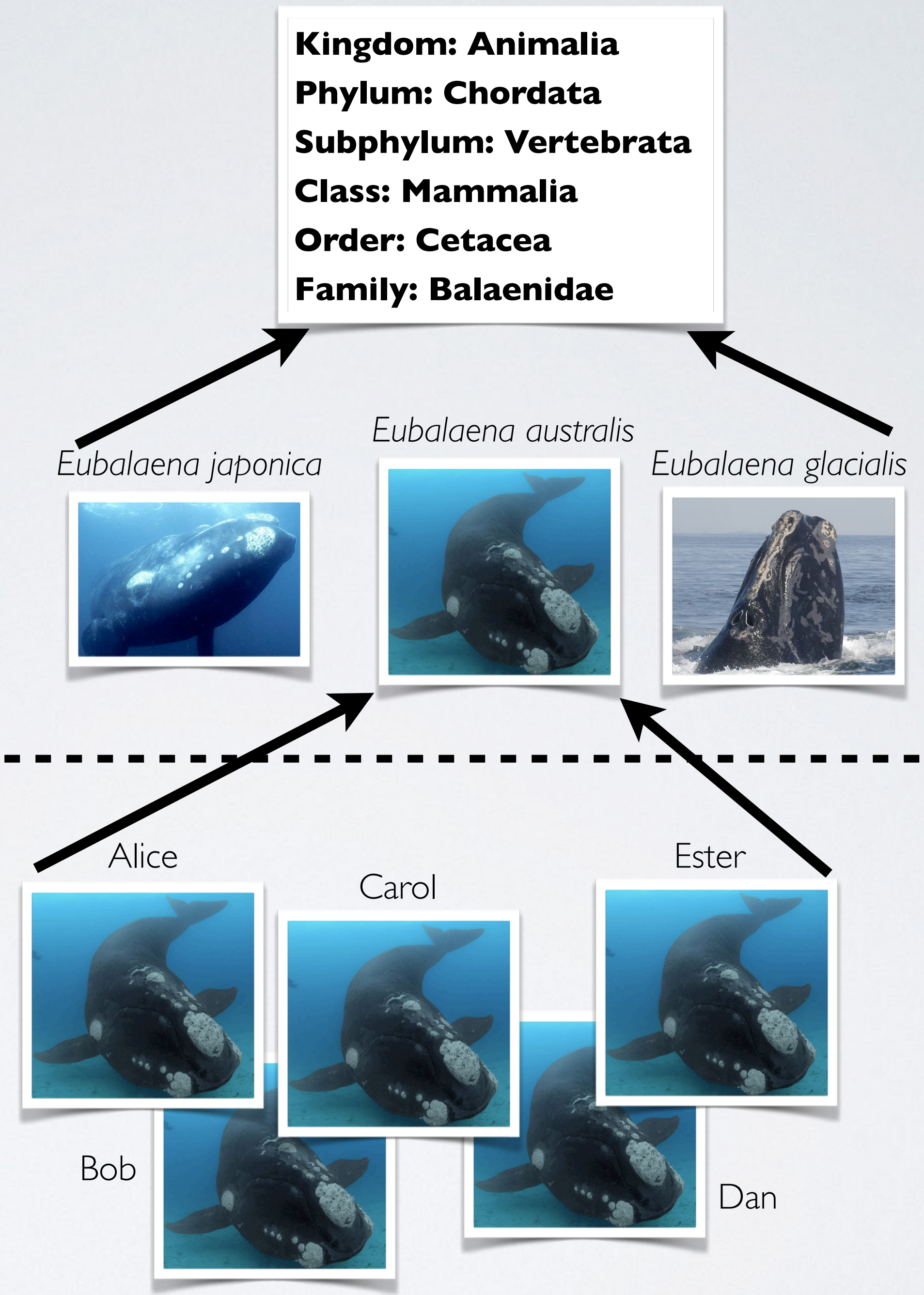


Macroevolution

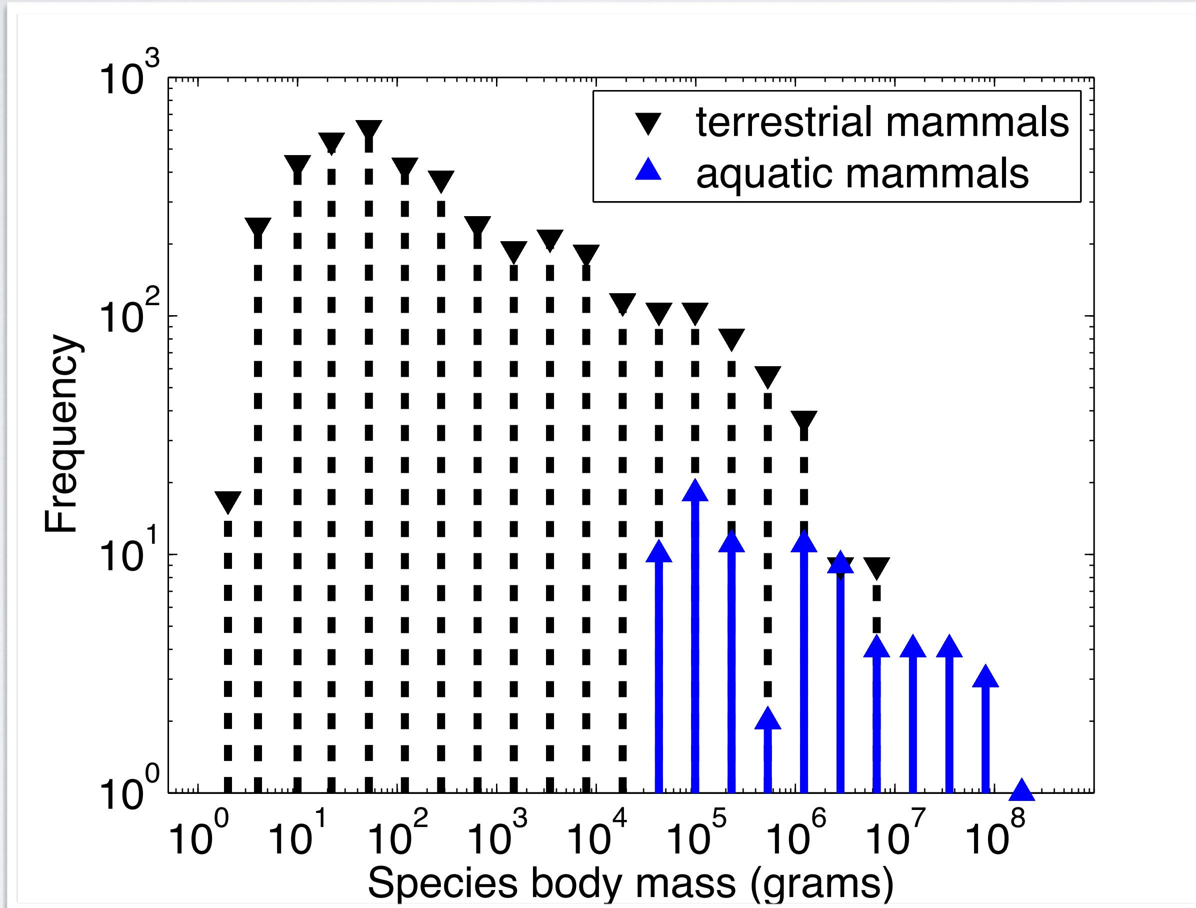
species level and above

Microevolution

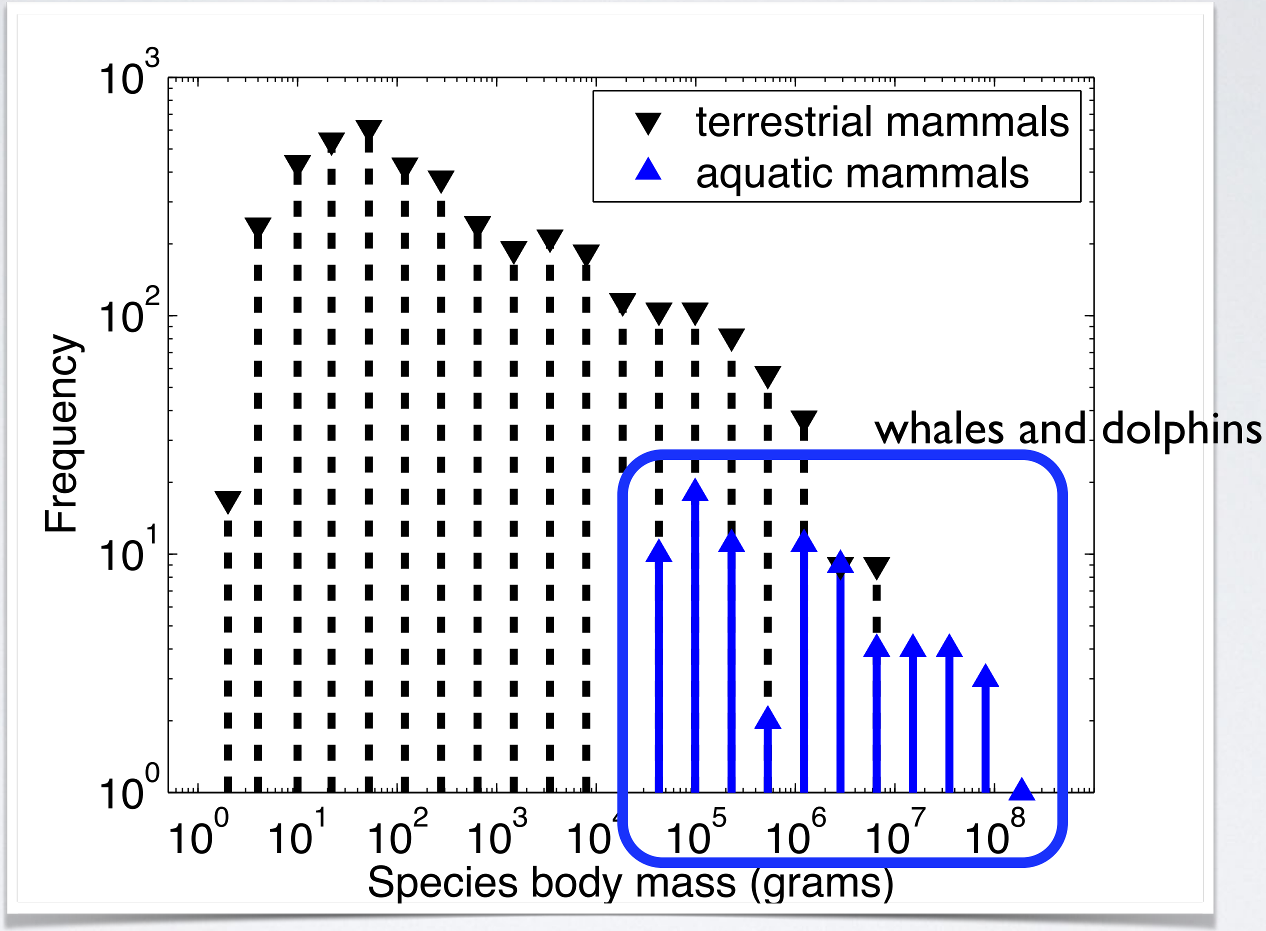
below species level



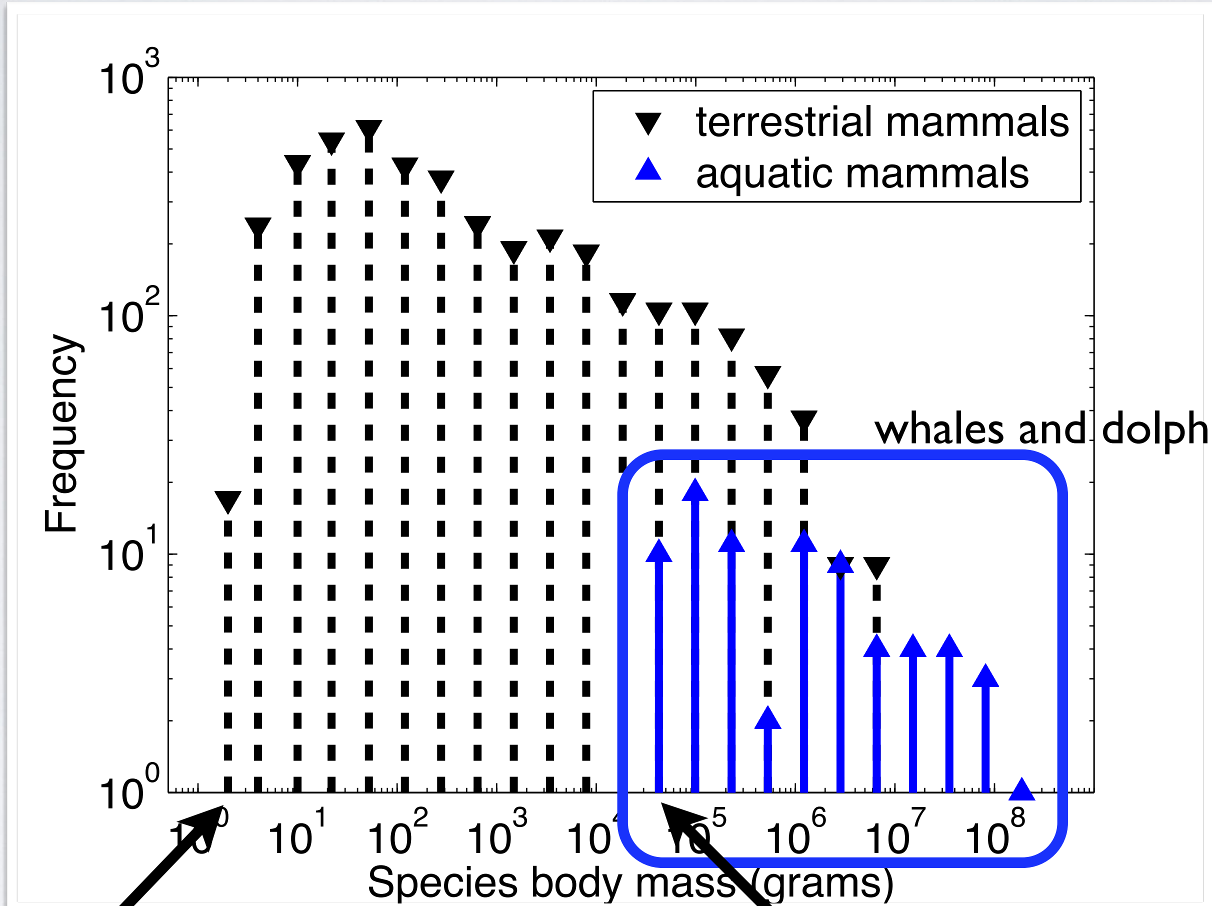
Mammal size diversity

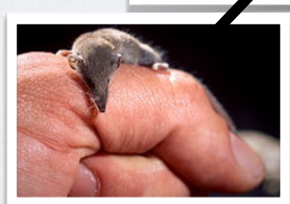


Mammal size diversity



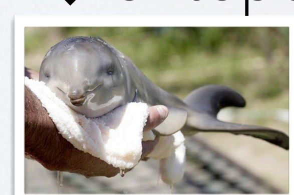
Terrestrial vs. aquatic



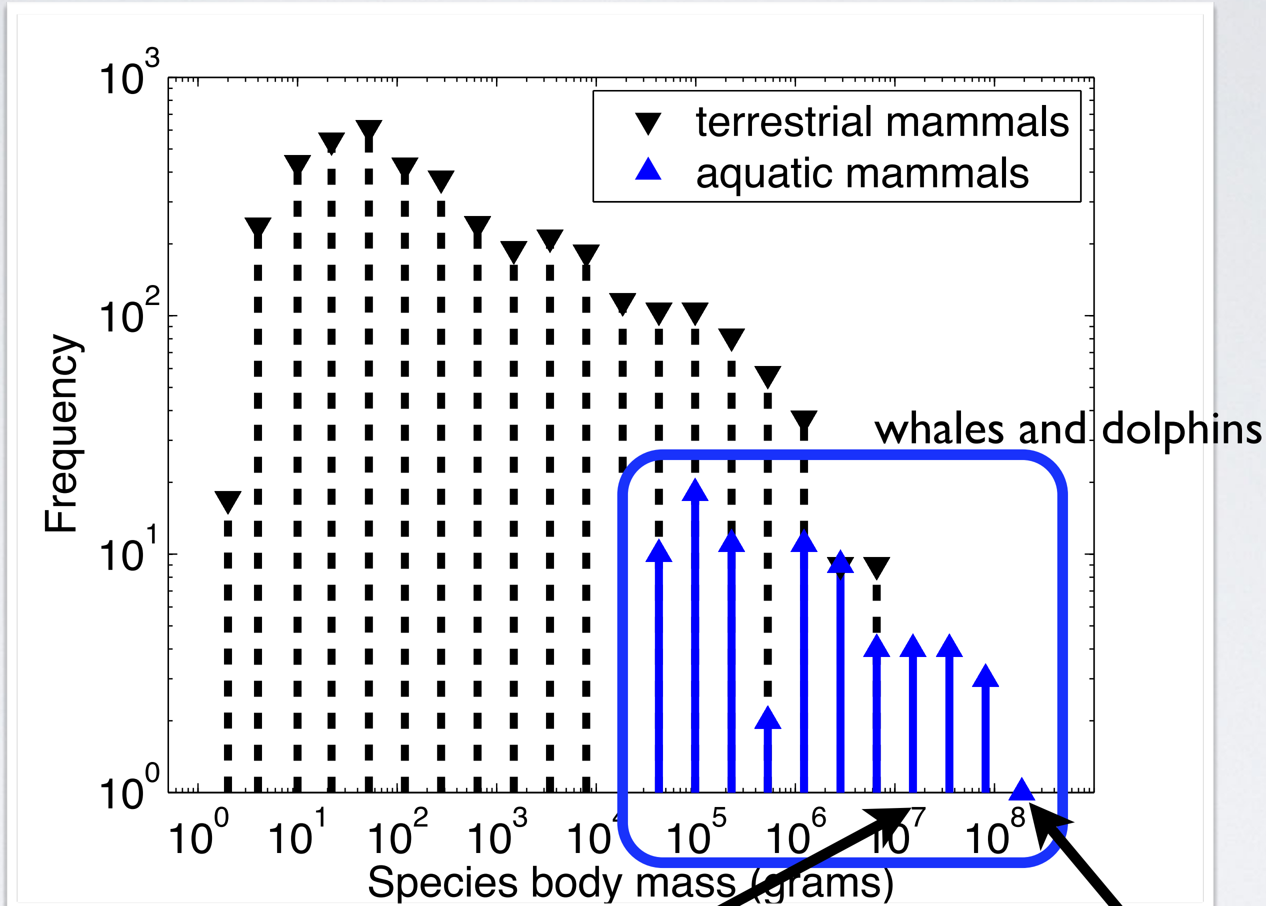


Suncus remyi (2g)

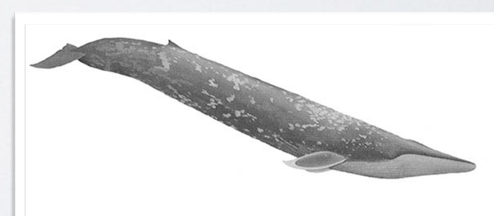
Pontoporia blainvillei (37,500g



Terrestrial vs. aquatic

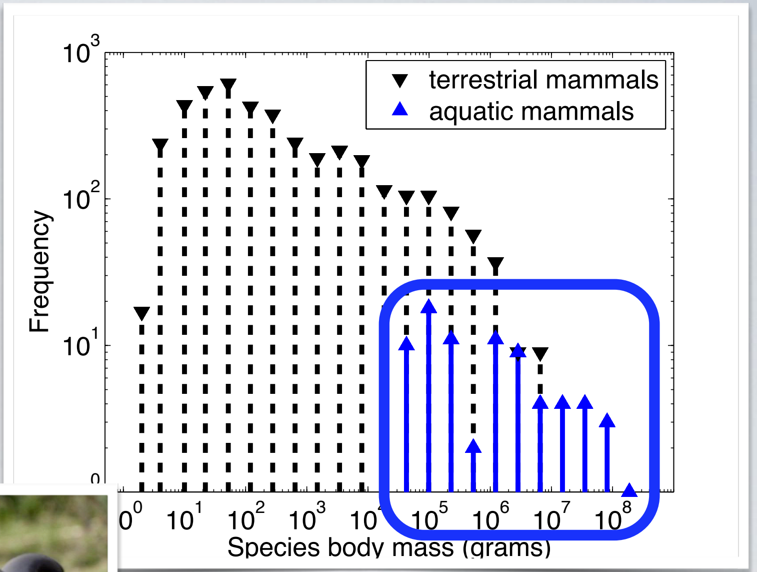


Loxodonta africana (10,000,000g)



Balaenoptera musculus (175,000,000g)

Terrestrial vs. aquatic



- minimum sizes

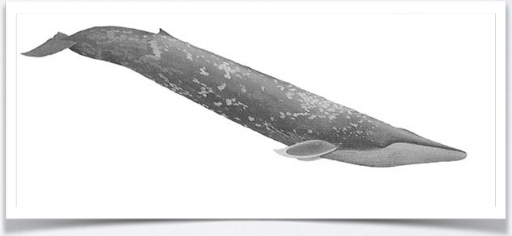
  Suncus remyi (2g)

  Pontoporia blainvillei (37,500g)

- maximum sizes

  Loxodonta africana (10,000,000g)

  Balaenoptera musculus (175,000,000g)



- diversity

  4001 species

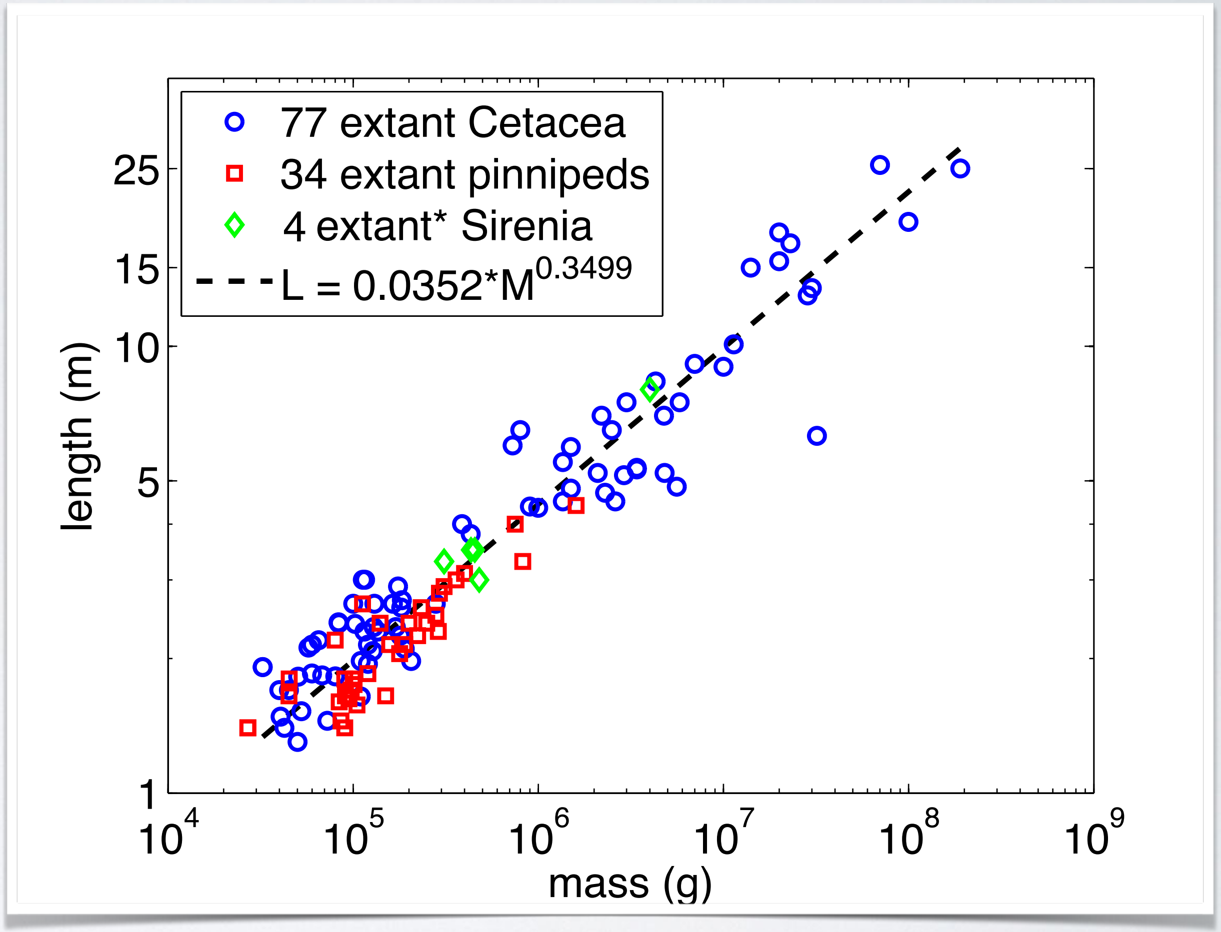
  77 species (Cetacea) [Sirenia = 4]

Impact of water on shape

- extant species only: whales, seals, otters, sea cows, etc.
- length L vs. mass M

Impact of water on shape

- extant species only: whales, seals, otters, sea cows, etc.
- length L vs. mass M
- consistent pattern = common evolutionary pressures on size
- okay to focus on Cetacea alone



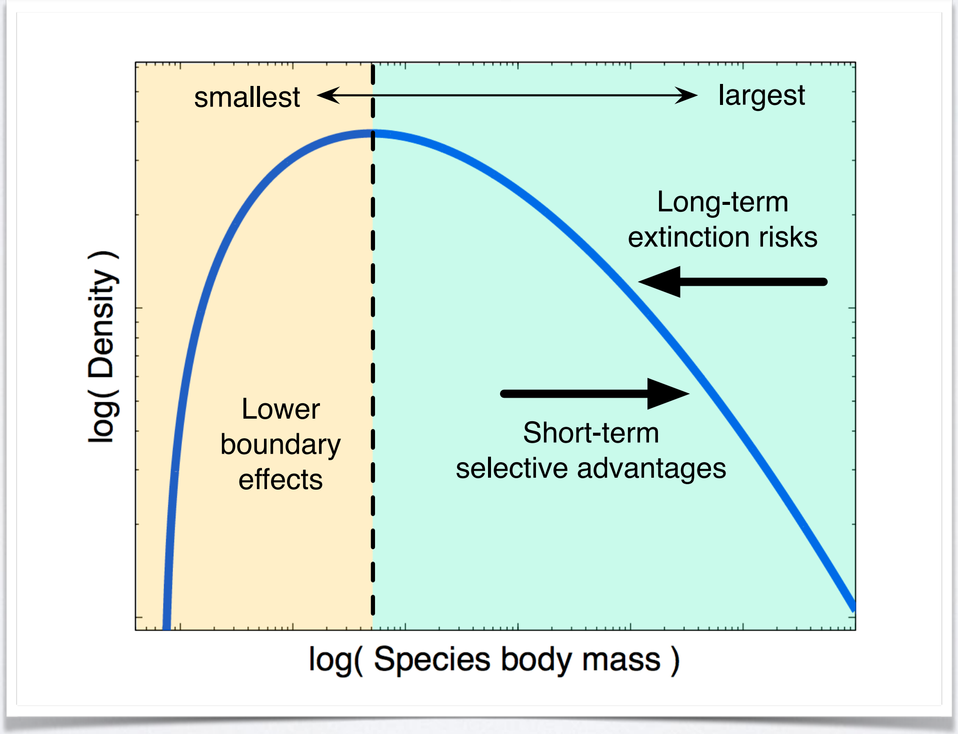
Central questions

- what processes drive terrestrial vs. aquatic size differences?
- a universal size-evolution explanation for both?
- what role for biomechanical / energetic constraints?

A macroevolutionary model of sizes

A macroevolutionary model of sizes

1. hard lower boundary = **physiology, metabolism**
2. biased diffusion = **short-term advantages**
3. size-dependent extinction rates = **long-term risks**



Clauset & Erwin, *Science* **321** (2008)
Clauset, Schwab & Redner, *Am. Nat.* **173** (2009)
Clauset & Redner, *Phys. Rev. Lett.* **102** (2009)

A macroevolutionary model of sizes

diffusion-reaction-convection: $x = \ln M$

$$\frac{\partial c}{\partial t} + \underbrace{v\frac{\partial c}{\partial x}}_{\substack{\text{drift term} \\ \text{(Cope's rule)}}} = \underbrace{D\frac{\partial^2 c}{\partial x^2}}_{\substack{\text{diffusion} \\ \text{term}}} + \underbrace{(k - A - Bx)c}_{\substack{\text{speciation} \\ \text{and extinction}}}$$

3 parameters:

$\beta = B/D$	extinction risk
$\mu = v/D$	strength of Cope's rule
$x_{\min}$	species minimum size

Clauset, Schwab & Redner, *Am. Nat.* **173** (2009)
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A macroevolutionary model of sizes

steady-state solution:

$$c(x) \propto \mathrm{e}^{\mu x/2} \mathrm{Ai}\left[\beta^{1/3}(x - x_{\min}) + z_0\right]$$

require first zero to go through $x_{\min}$

$$z_0 = -2.3381\ldots$$

3 parameters:

$\beta = B/D$	extinction risk
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$x_{\min}$	species minimum size

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Clauset & Redner, *Phys. Rev. Lett.* **102** (2009)

Comments

ecology-free

- no inter-specific interaction (competition, predation, etc.)
- no population dynamics
- no anagenetic variation of body size

environment-free

- no climatic dependencies
- no geography

mass-extinction-free

Past results: terrestrial mammals

$$c(x) \propto \mathrm{e}^{\mu x/2} \mathrm{Ai}\left[\beta^{1/3}(x - x_{\min}) + z_0\right]$$

$\beta \approx 0.08$ fitted

$\mu \approx 0.2$ Alroy (2001)

$M_{\min} = 2\mathrm{g}$ Pearson (1948)

4001 terrestrial species

Clauset, Schwab & Redner, *Am. Nat.* **173** (2009)
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terrestrial mammal size data from Smith et al. (2003)

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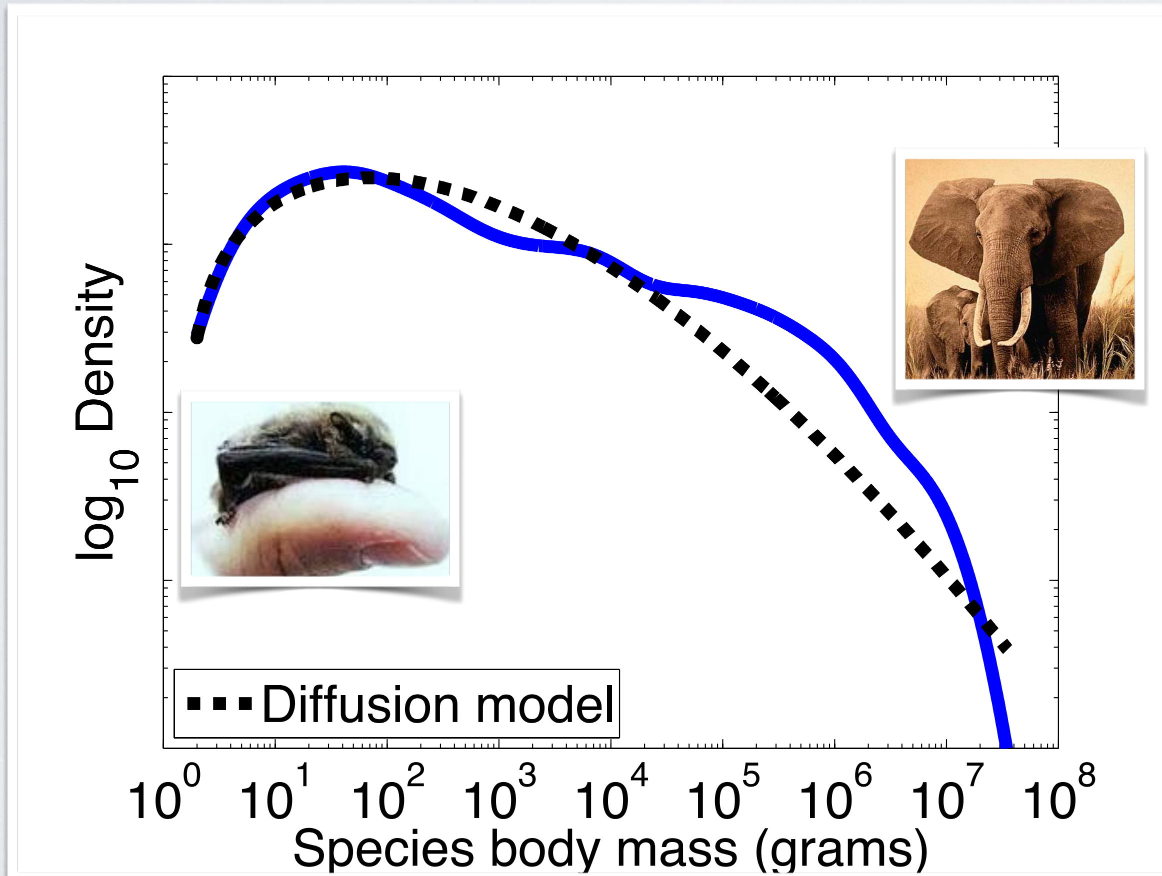

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Model structure

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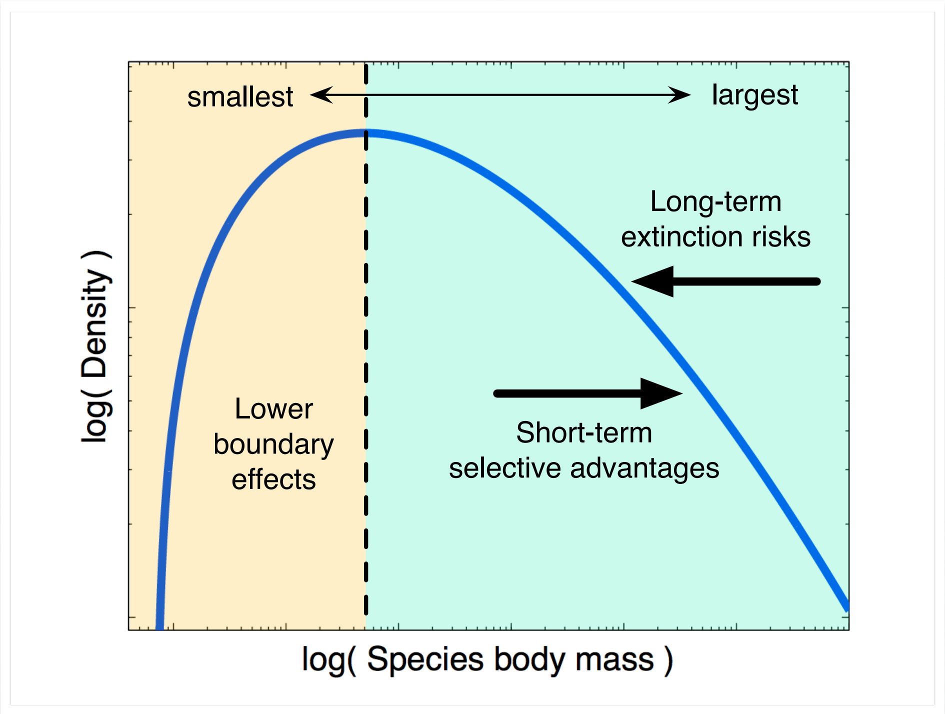
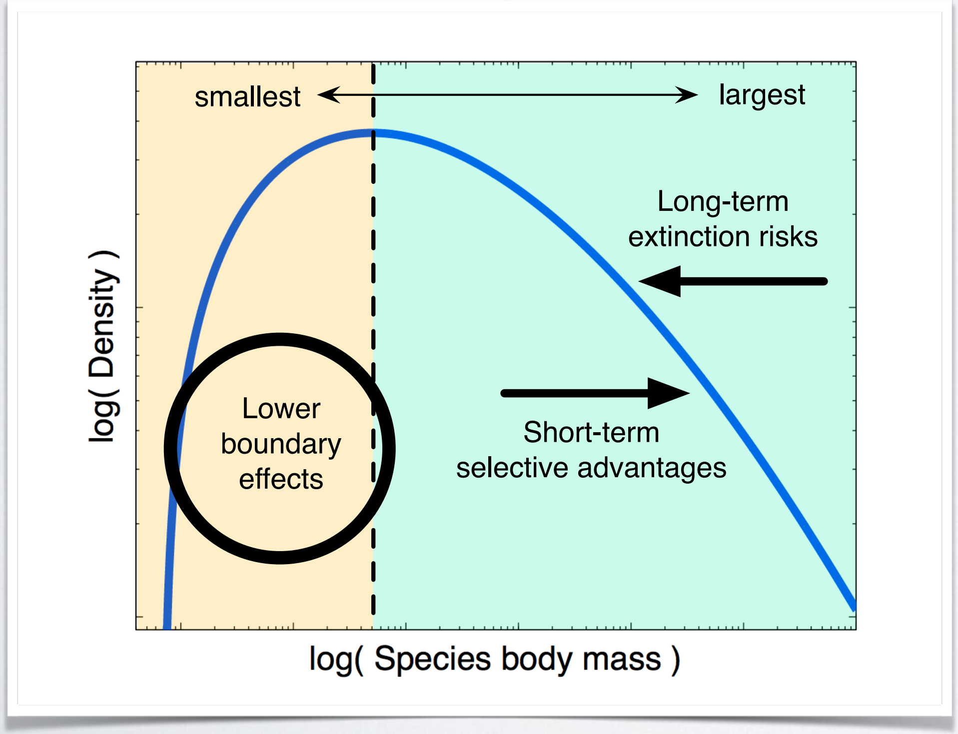


Model structure

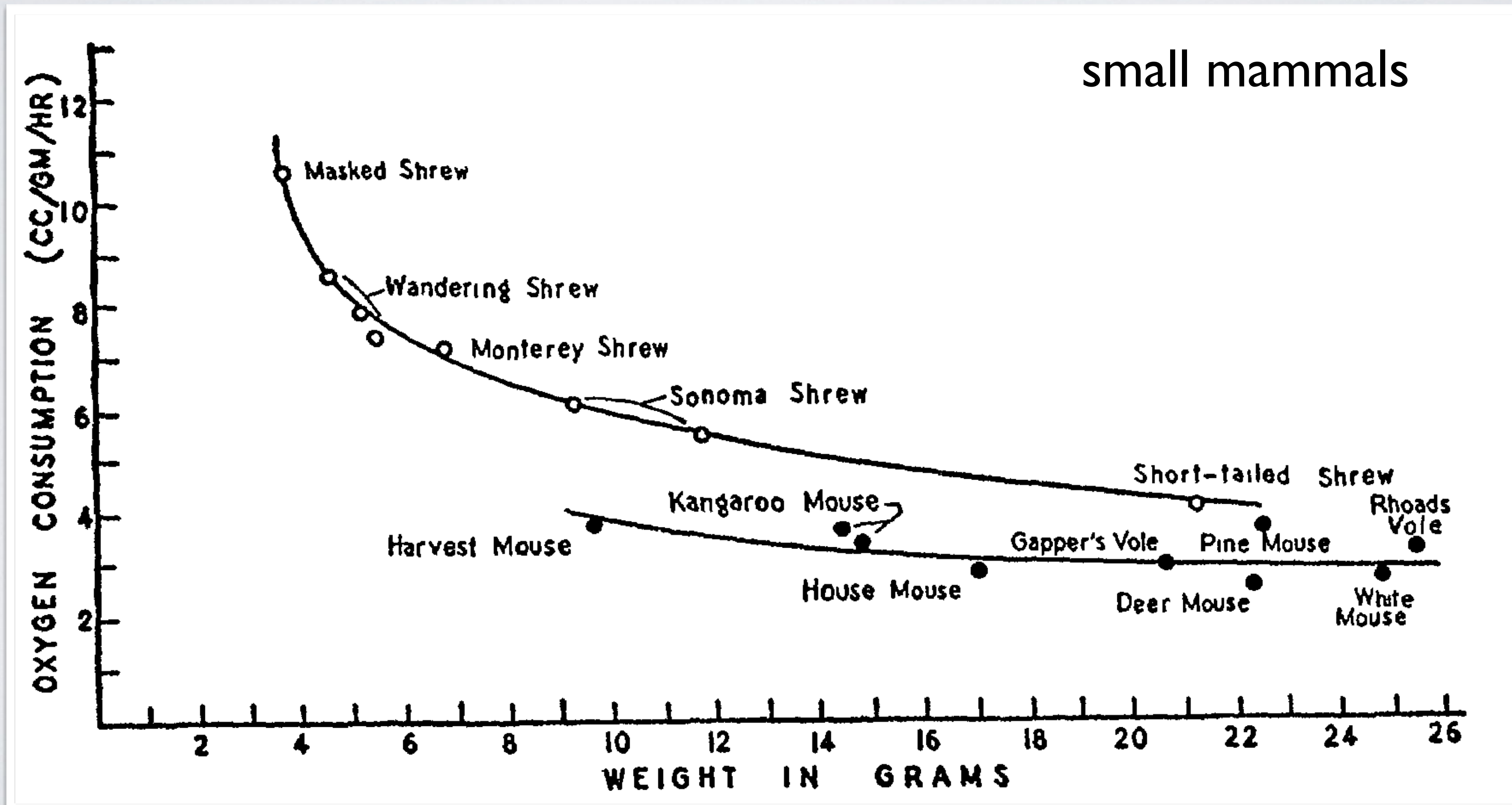
1. hard lower boundary = **physiology, metabolism**

thermoregulation: air vs. water



Terrestrial mammals : air

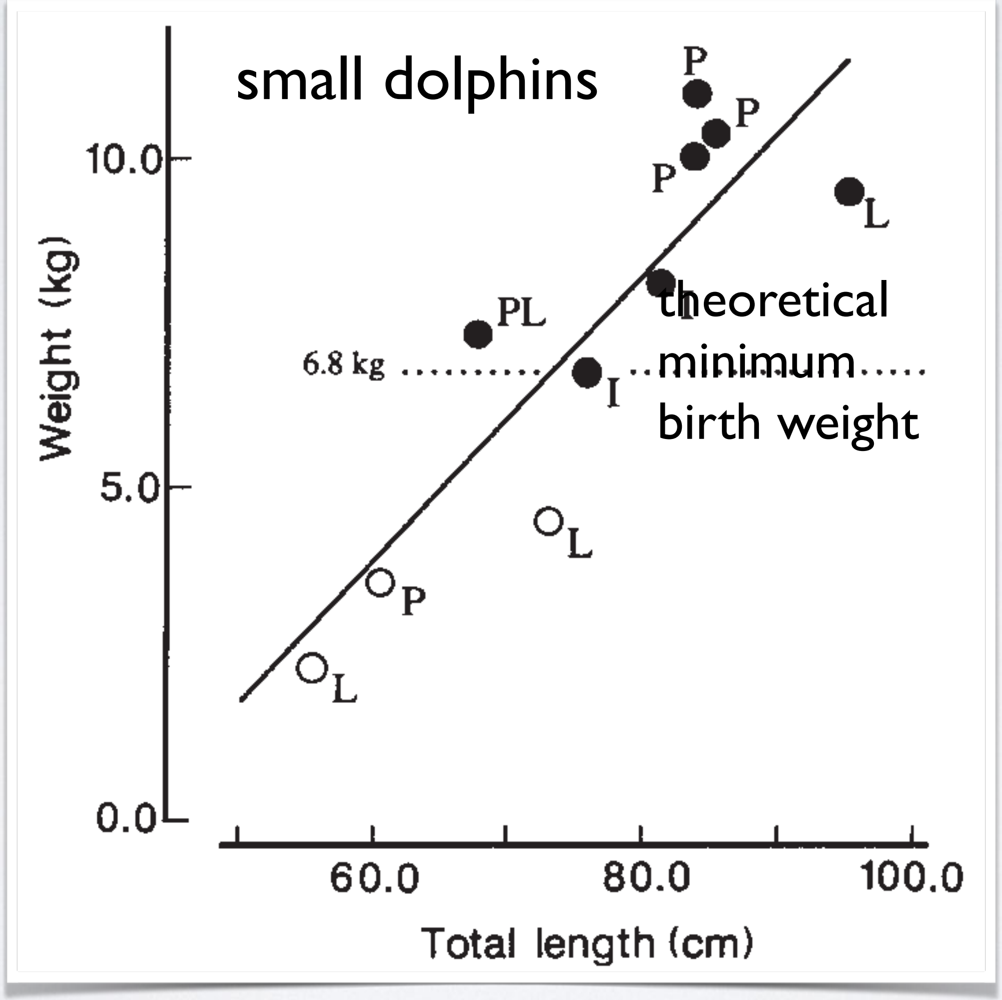
thermoregulation constraints $\longrightarrow M_{\rm min} \approx 2{\rm g}$



from Pearson (1948)

Aquatic mammals : water

thermoregulation constraints $\longrightarrow M_{\min} \approx 7000\text{g}$



from Downhower & Blumer (1988)

A model for whales

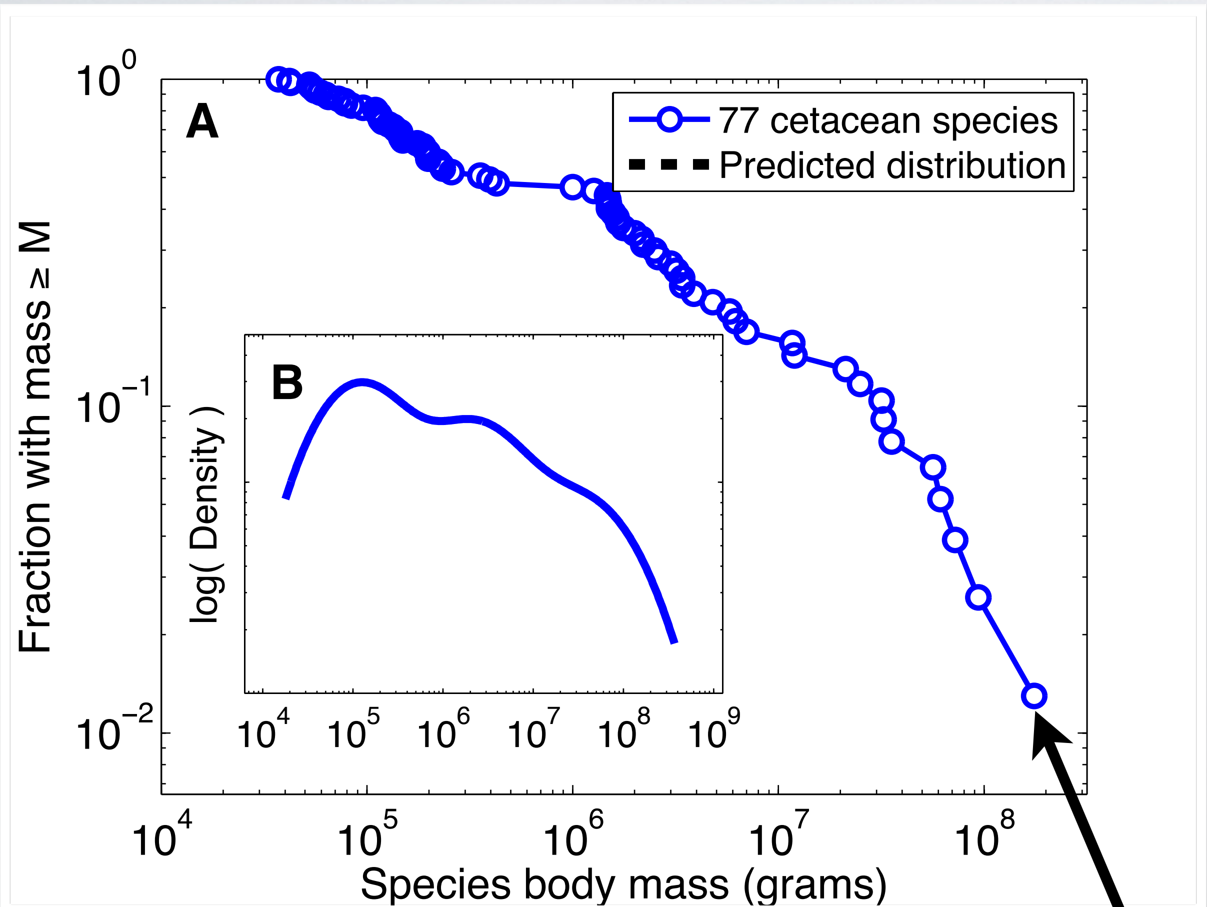
1. accurate extant whale size data
2. specify model
   1. shift $M_{\min} \to 7000\text{kg}$
   2. use terrestrial μ ,β
   3. steady-state prediction $c(x) = \Pr(\ln M \mid \mu, \beta, \ln M_{\min})$
3. compare $\Pr(\ln M)$ with data
4. compare expected maximum with Blue Whale M_*

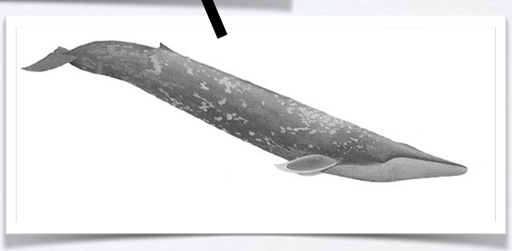
Cetacaen data

- 77 species
- 183 mass measurements
  [2.4 per species]
- constructed from scientific literature

group	family	species	mass_kg	primary source (reference)
Mysticeti	Balaenidae	Balaena mysticetus	100000	Smith_etal_2003
Mysticeti	Balaenidae	Balaena mysticetus	87500	Jefferson_Leatherwood_Webber_1993
Mysticeti	Balaenidae	Eubalaena australis	23000	Smith_etal_2003
Mysticeti	Balaenidae	Eubalaena australis	100000	Jefferson_Leatherwood_Webber_1993
Mysticeti	Balaenidae	Eubalaena glacialis	23000	Smith_etal_2003
Mysticeti	Balaenidae	Eubalaena glacialis	90000	Jefferson_Leatherwood_Webber_1993
Mysticeti	Balaenopteridae	Balaenoptera acutorostrata	10000	Smith_etal_2003
Mysticeti	Balaenopteridae	Balaenoptera acutorostrata	14000	Jefferson_Leatherwood_Webber_1993
				Perrin_Zubtsova_Kuzmin_2004
Mysticeti	Balaenopteridae	Balaenoptera borealis	20000	Smith_etal_2003
Mysticeti	Balaenopteridae	Balaenoptera borealis	30000	Jefferson_Leatherwood_Webber_1993
				Long_1968
Mysticeti	Balaenopteridae	Balaenoptera edeni	20000	Smith_etal_2003
Mysticeti	Balaenopteridae	Balaenoptera edeni	22500	Jefferson_Leatherwood_Webber_1993
Mysticeti	Balaenopteridae	Balaenoptera musculus	190000	Smith_etal_2003
Mysticeti	Balaenopteridae	Balaenoptera musculus	160000	Jefferson_Leatherwood_Webber_1993
				Morton_ed_1997
Mysticeti	Balaenopteridae	Balaenoptera physalus	70000	Smith_etal_2003
Mysticeti	Balaenopteridae	Balaenoptera physalus	75000	Jefferson_Leatherwood_Webber_1993
				Uhen_Fordyce_Barnes_1998_inJanisGu
				ellUhen
Mysticeti	Balaenopteridae	Megaptera novaeangliae	30000	Smith_etal_2003
Mysticeti	Balaenopteridae	Megaptera novaeangliae	35000	Jefferson_Leatherwood_Webber_1993
				Clapham_Mead_1999,
				Uhen_Fordyce_Barnes_1998_inJanisGu
				ellUhen
Mysticeti	Eschrichtiidae	Eschrichtius robustus	28500	Smith_etal_2003
Mysticeti	Eschrichtiidae	Eschrichtius robustus	35000	Jefferson_Leatherwood_Webber_1993
				Uhen_Fordyce_Barnes_1998_inJanisGu
				ellUhen
Mysticeti	Neobalaenidae	Caperea marginata	3200	Jefferson_Leatherwood_Webber_1993
				Perrin_Zubtsova_Kuzmin_2004
Odontoceti	Delphinidae	Cephalorhynchus commersonii	72.4	Smith_etal_2003
Odontoceti	Delphinidae	Cephalorhynchus commersonii	76	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Cephalorhynchus commersonii	86	Culik_2004
Odontoceti	Delphinidae	Cephalorhynchus eutropia	45	Smith_etal_2003
Odontoceti	Delphinidae	Cephalorhynchus eutropia	63	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Cephalorhynchus eutropia	60	Culik_2004
Odontoceti	Delphinidae	Cephalorhynchus heavisidii	40	Smith_etal_2003
Odontoceti	Delphinidae	Cephalorhynchus heavisidii	65	Culik_2004
Odontoceti	Delphinidae	Cephalorhynchus hectori	50	Smith_etal_2003
Odontoceti	Delphinidae	Cephalorhynchus hectori	57	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Delphinus delphis	80	Smith_etal_2003
Odontoceti	Delphinidae	Delphinus delphis	135	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Delphinus delphis	200	Culik_2004
Odontoceti	Delphinidae	Feresa attenuata	170	Smith_etal_2003
Odontoceti	Delphinidae	Feresa attenuata	225	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Globicephala macrorhynchus	726	Smith_etal_2003
Odontoceti	Delphinidae	Globicephala macrorhynchus	3600	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Globicephala melas	800	Smith_etal_2003
Odontoceti	Delphinidae	Globicephala melas	2000	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Globicephala melas	1600	Perrin_Zubtsova_Kuzmin_2004
Odontoceti	Delphinidae	Grampus griseus	387.5	Smith_etal_2003
Odontoceti	Delphinidae	Grampus griseus	400	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Lagenodelphis hosei	164	Smith_etal_2003
Odontoceti	Delphinidae	Lagenodelphis hosei	210	Jefferson_Leatherwood_Webber_1993
Odontoceti	Delphinidae	Lagenodelphis hosei	210	Culik_2004

A model for whales

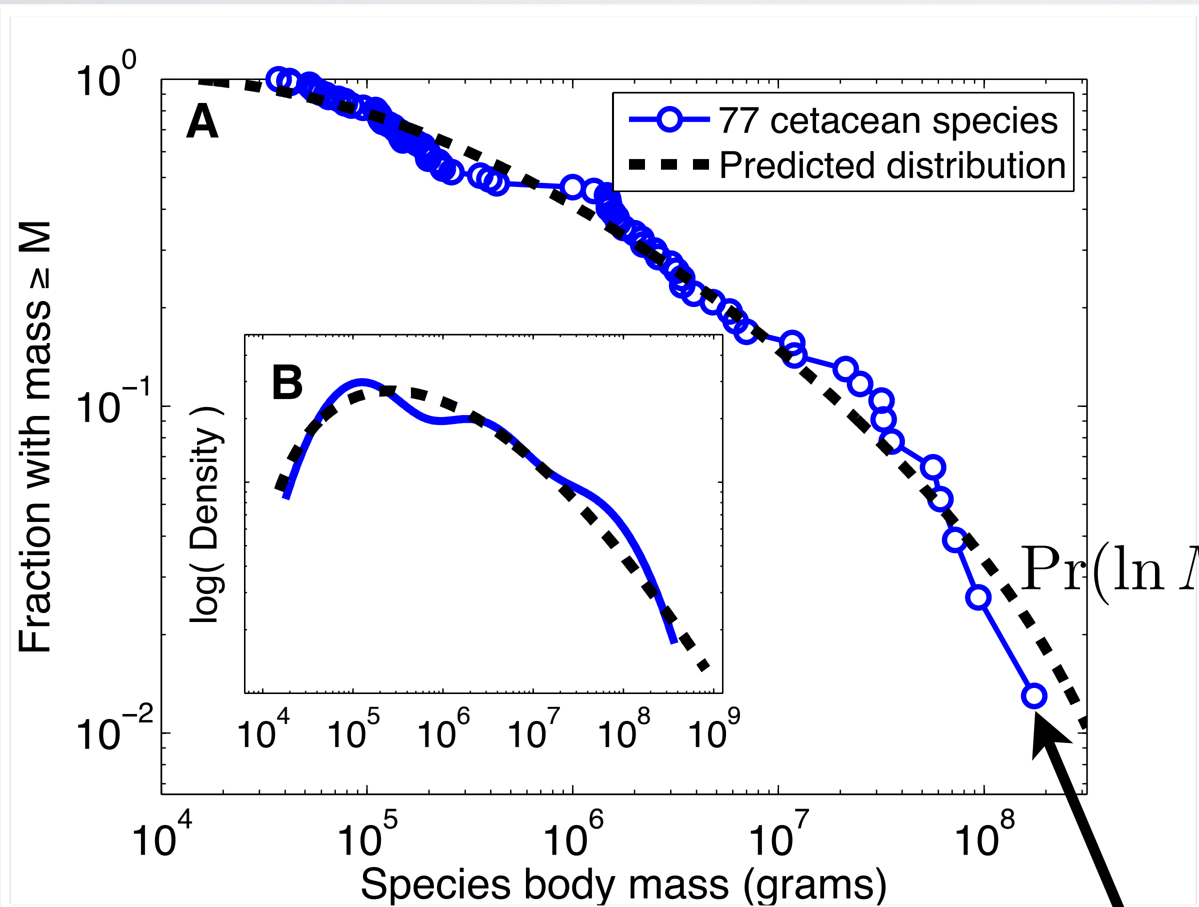




$$\left.\begin{array}{l}\beta \approx 0.08 \\ \mu \approx 0.2\end{array}\right\}$$ from terrestrial model

$$M_{\min} = 7000\text{kg}$$ Downhower & Blumer (1988)

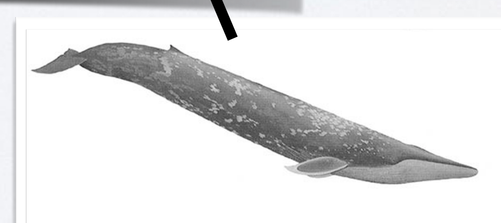
A model for whales



$$\left.\begin{array}{l}\beta \approx 0.08 \\ \mu \approx 0.2\end{array}\right\}$$ from terrestrial model

$M_{\min} = 7000\text{kg}$ Downhower & Blumer (1988)

$\Pr(\ln M)$



A model for whales

good fit! but how good?

- hypothesis test against $\Pr(\ln M)$
- compare expected maximum with Blue Whale M_*

Hypothesis test

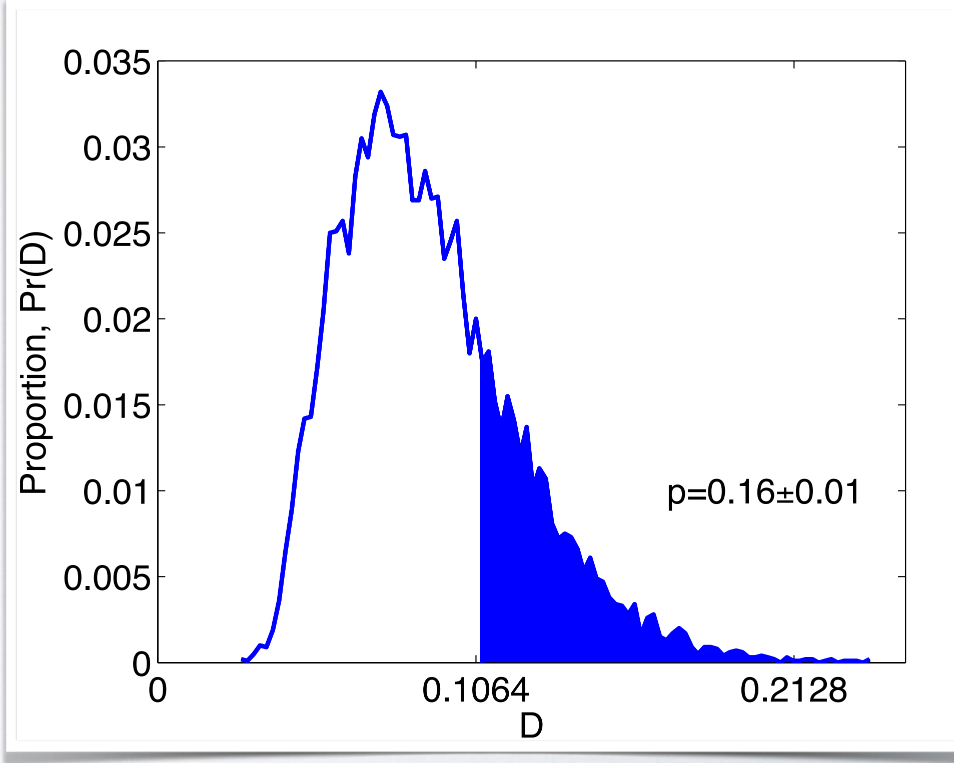
good fit! but how good?

- compute D^*, KS distance from data to null $\Pr(\ln M)$
- draw $n = 77$ sizes from $\Pr(\ln M)$
- measure KS distance D from $\Pr(\ln M)$
- repeat $= \Pr(D)$
- $p = \Pr(D \geq D^*)$

using whales data

➤ $p = 0.16 \pm 0.01$

➤ indistinguishable from model



Largest expected whale test

compare expected maximum with Blue Whale $M_* = 1.75 \times 10^8 \mathrm{g}$

- classic large-deviation calculation
- $\Pr(M_*) = 1 - \left(\int_{M_{\min}}^{M_*} \Pr(M) \mathrm{d}M \right)^n$

using whales data

- ➤ $\Pr(M_*) = 0.88 \pm 0.03$
- ➤ at least one Blue Whale or larger is expected

Largest expected whale test

compare expected maximum with Blue Whale $M_* = 1.75 \times 10^8\mathrm{g}$

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- $\Pr(M_*) = 1 - \left(\int_{M_{\min}}^{M_*} \Pr(M)\mathrm{d}M \right)^n$

using whales data

- ➤ $\Pr(M_*) = 0.88 \pm 0.03$
- ➤ at least one Blue Whale or larger is expected
- ➤ expected maximum size is $\mathrm{E}[M_*] = 6.48 \times 10^8\mathrm{g}$

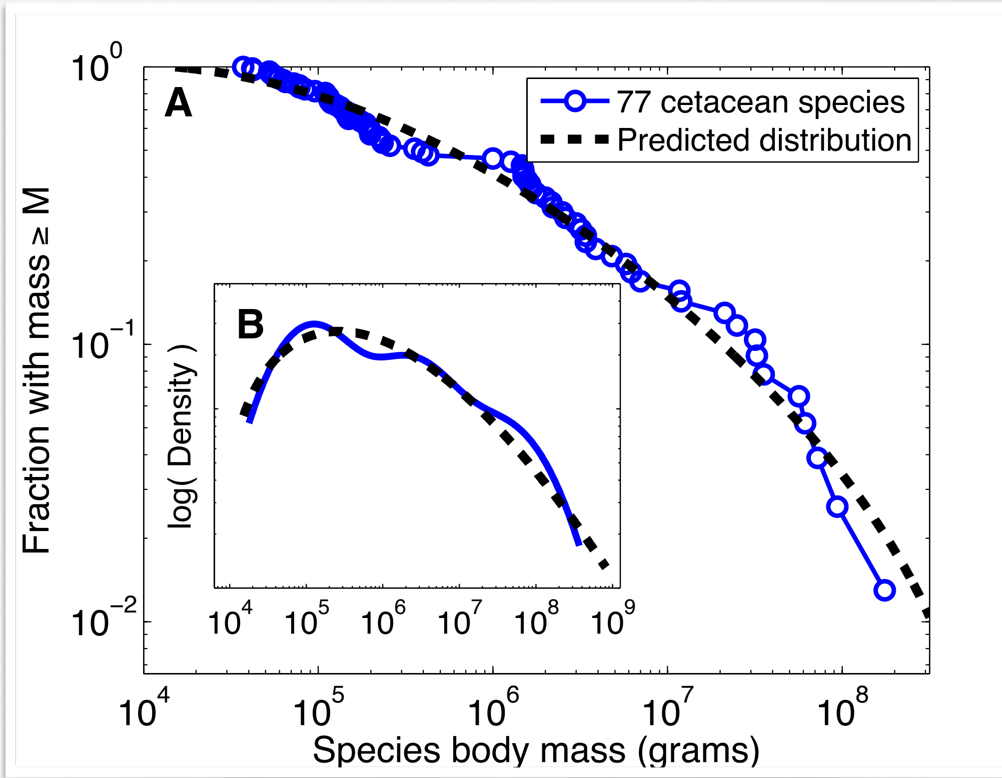
Conclusions

How large should whales be?

- exactly the sizes they are (maybe a little bigger)
- mammal sizes + aquatic life (shifted $M_{\min}$)
- zero-parameter macroevolutionary prediction
- energetic constraints play secondary role

what now?

- "macroevolutionary conveyor belt of death"
- climate change?
- other groups? (horses...)



thanks

- Cris Moore
- Josh Ladau
- Doug Erwin
- Alison Boyer
- Felissa Smith
- Nick Peynson
- Lauren Shoemaker
- Santa Fe Institute

further reading:

Body mass evolution and diversification within the *Equidae* family
with L. Shoemaker *in prep* (2013)

How large should whales be?
- *PLOS ONE* (2013) arxiv:1207.1478

Evolutionary model of species body mass diversification
with S. Reder *Physical Review Letters* (2009) arxiv:0808.4014

How many species have mass *M*?
with D.J. Schwab & S. Redner *American Naturalist* (2009) arxiv:0808.3433

The evolution and distribution of species body size
with D.H. Erwin *Science* **321** (2008) arxiv:0901.0251


fin

ECOLOGY LETTERS

Ecology Letters, (2014) **17**: 211–220 doi: 10.1111/ele.12221

LETTER

Body mass evolution and diversification within horses (family Equidae)

Lauren Shoemaker[1,2] and Aaron Clauset[2,3,4]*

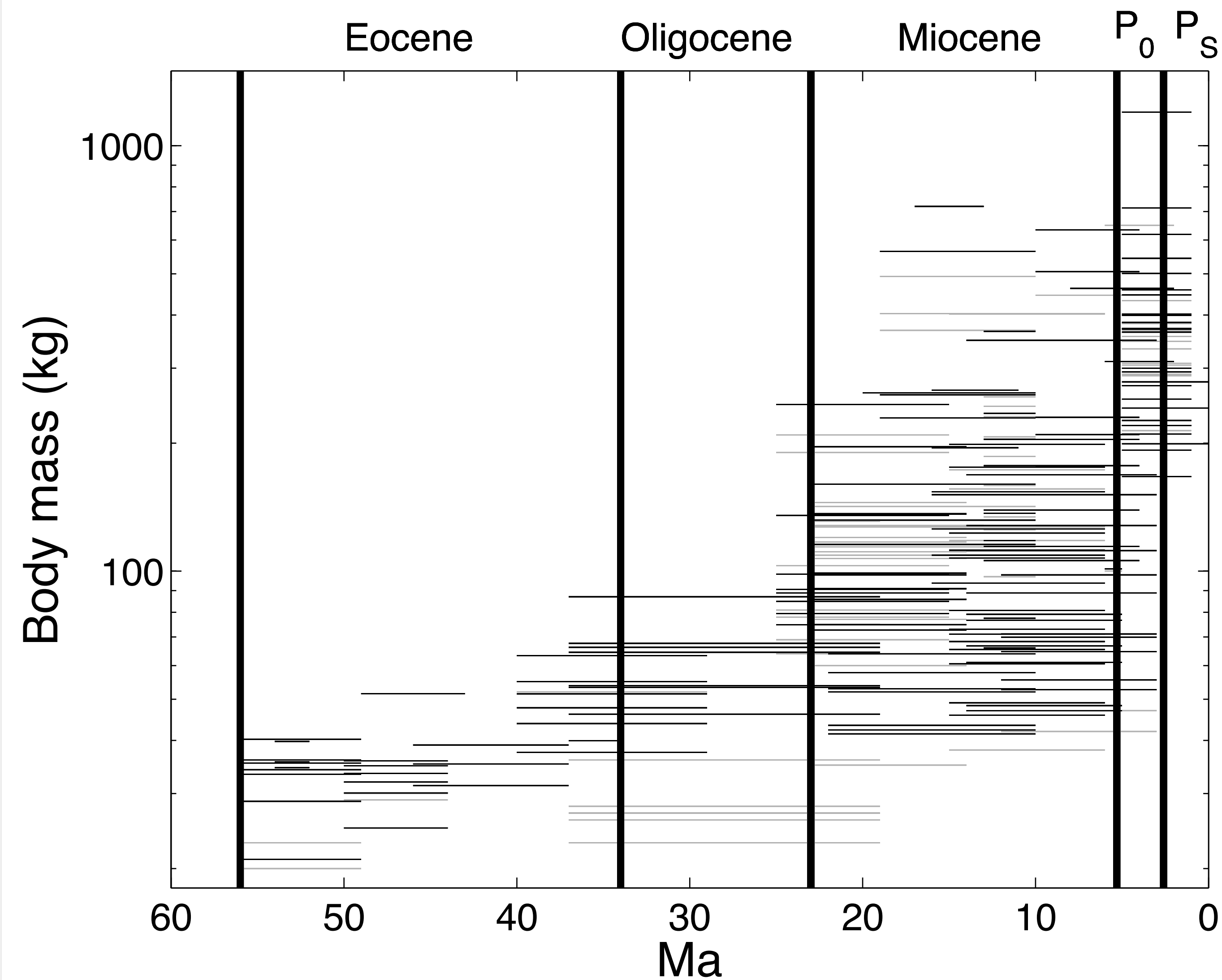
Abstract

Horses (family Equidae) are a classic example of adaptive radiation, exhibiting a nearly 60-fold increase in maximum body mass and a peak taxonomic diversity of nearly 100 species across four continents. Such patterns are commonly attributed to niche competition, in which increased taxonomic diversity drives increased size disparity. However, neutral processes, such as macroevolutionary 'diffusion', can produce similar increases in disparity without increased diversity. Using a comprehensive database of Equidae species size estimates and a common mathematical framework, we measure the contributions of diversity-driven and diffusion-driven mechanisms for increased disparity during the Equidae radiation. We find that more than 90% of changes in size disparity are attributable to diffusion alone. These results clarify the role of species competition in body size evolution, indicate that morphological disparity and species diversity may be only weakly coupled in general, and demonstrate that large species may evolve from neutral macroevolutionary diffusion processes alone.

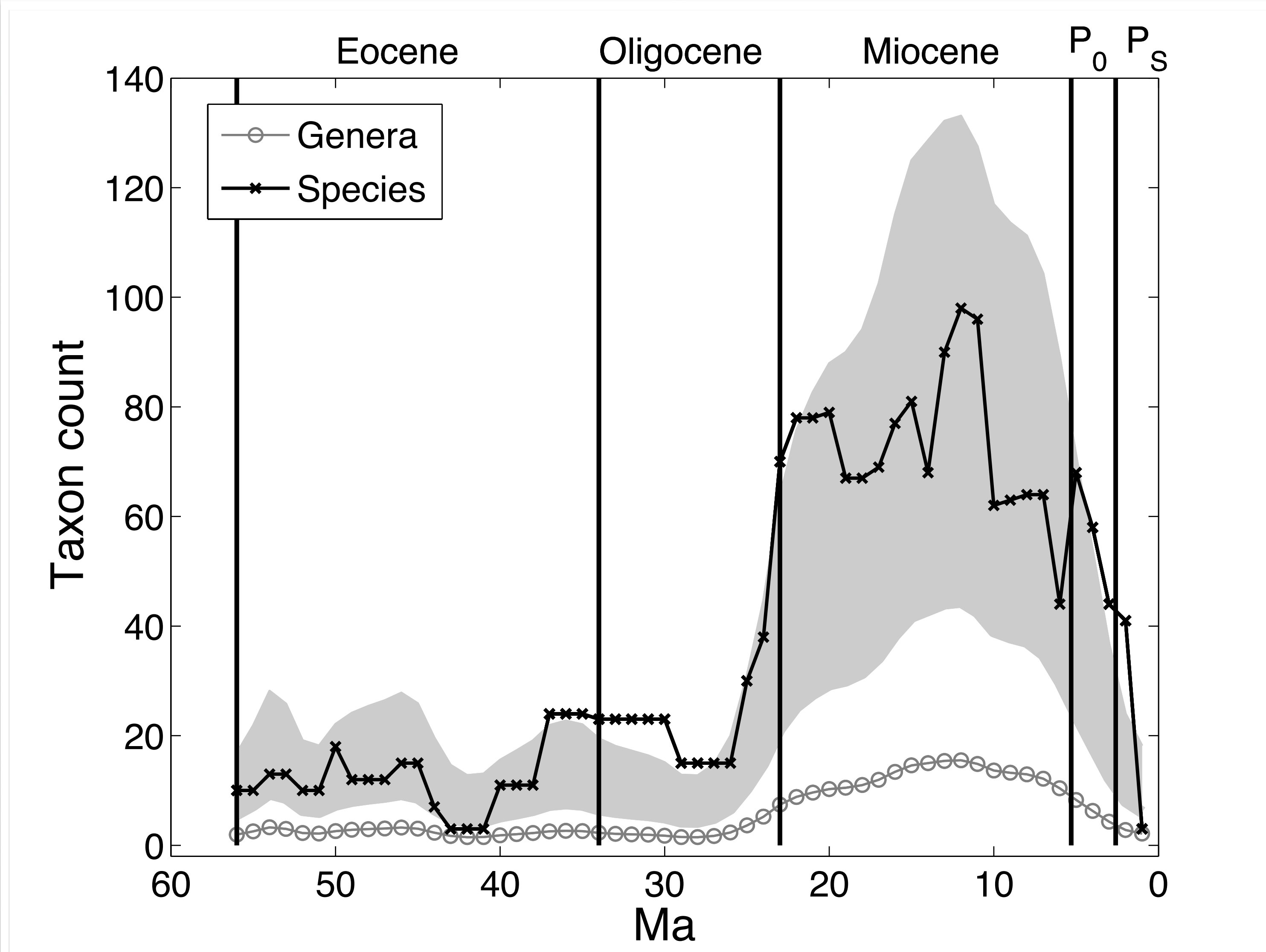
Keywords

Adaptive radiation, body mass distributions, Equidae, macroevolution, mathematical models, size disparity.

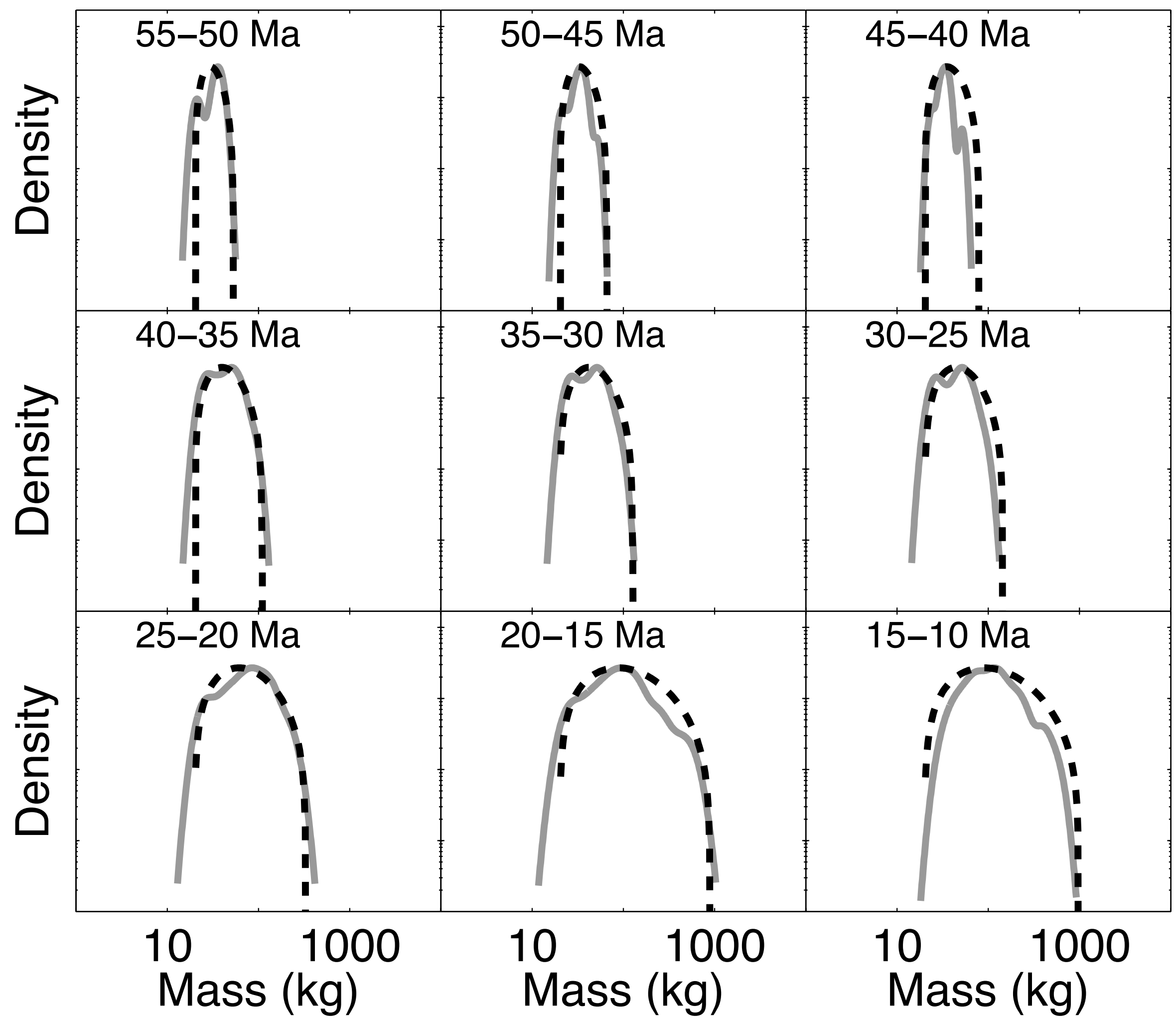
Ecology Letters (2014) **17**: 211–220



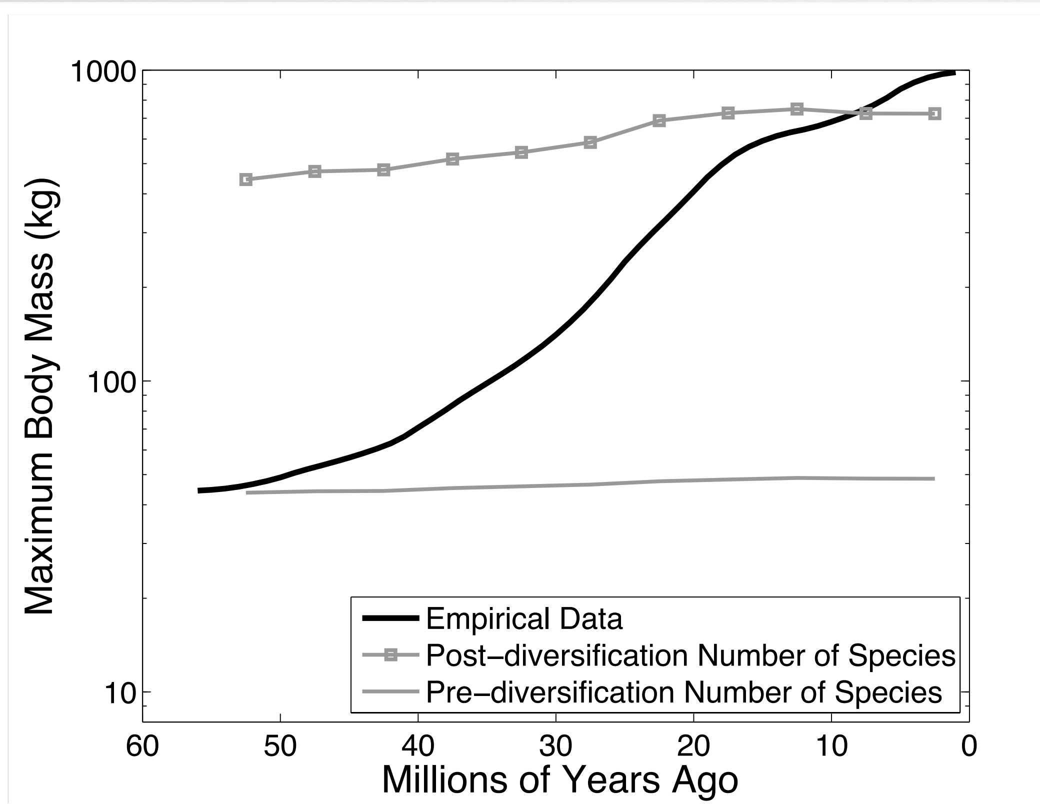
Eocene
Oligocene
Miocene
P_0
P_S
Body mass (kg)
1000
100
60
50
40
30
20
10
0
Ma



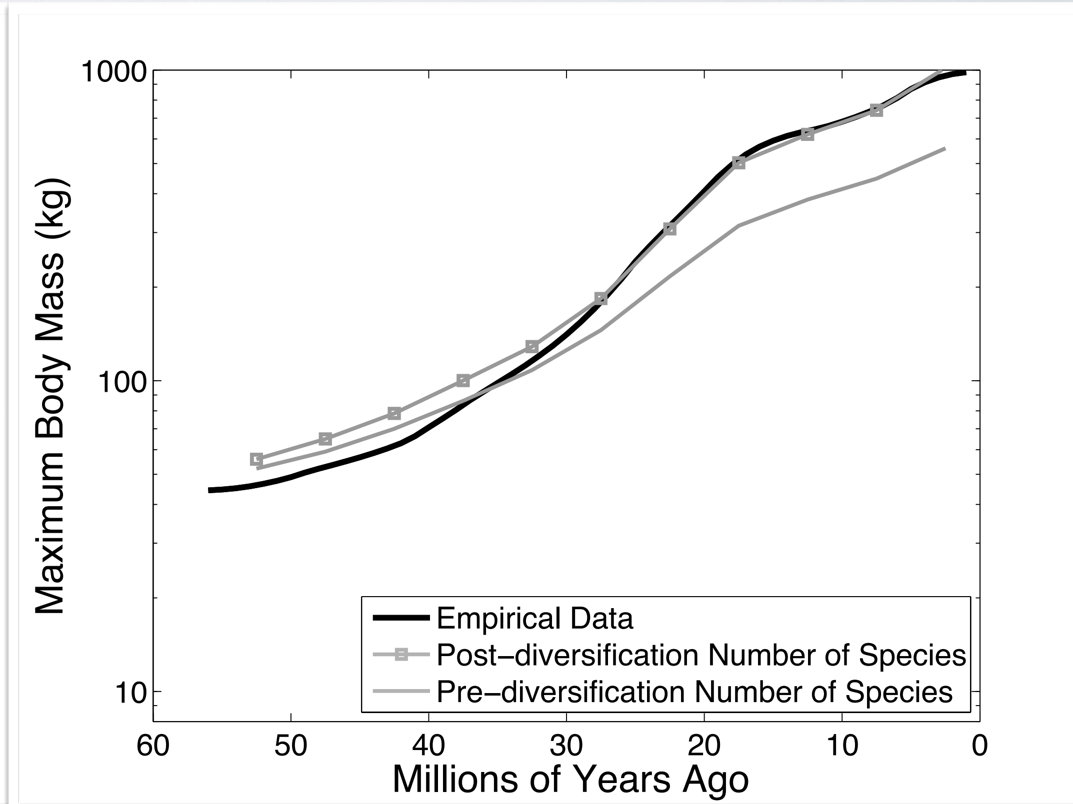
Eocene
Oligocene
Miocene
P_0
P_S
Genera
Species
Taxon count
Ma
140
120
100
80
60
40
20
0
60
50
40
30
20
10
0



55–50 Ma
50–45 Ma
45–40 Ma
40–35 Ma
35–30 Ma
30–25 Ma
25–20 Ma
20–15 Ma
15–10 Ma
Density
Density
Density
10
1000
10
1000
10
1000
Mass (kg)
Mass (kg)
Mass (kg)



Maximum Body Mass (kg)
1000
100
10
60
50
40
30
20
10
0
Millions of Years Ago
Empirical Data
Post−diversification Number of Species
Pre−diversification Number of Species



Maximum Body Mass (kg)
1000
100
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60
50
40
30
20
10
0
Millions of Years Ago
Empirical Data
Post−diversification Number of Species
Pre−diversification Number of Species