Biological scaling theory and effects on populations

By
Van Savage
Department of Systems Biology
Harvard Medical School

Beijing CSSS, 2007

Outline

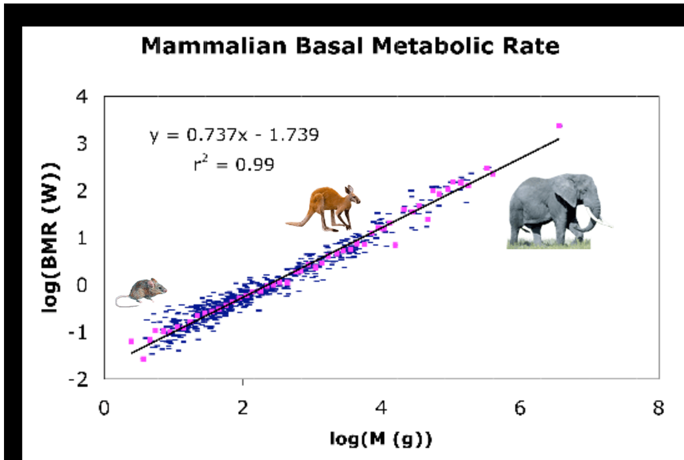
1. Theory for dependence of biological rates, times, and lengths on body size

2. Dependence for biological rates on body temperature

3. Scaling or population growth

4. Scaling of species interactions (predator-prey)

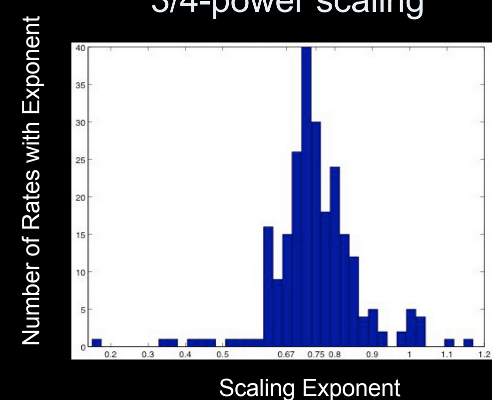
5. Conclusions



$$B = B_0 M^{3/4}$$

Savage, et al., *Func. Eco.*, 2004

3/4-power scaling



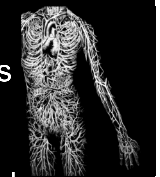
Rates at the cellular, individual, and population level for many different taxa scale like this. Many times and lengths also scale.

Savage et al., *Func. Eco.*, 2004; Peters, *Ecol. Implications of Body Size*, (1983)

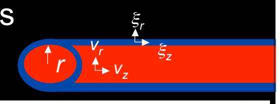
Theory for body mass scaling

Theory has three assumptions

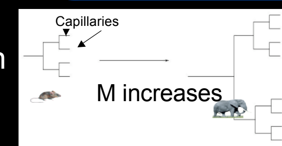
i. Branching, hierarchical network that is space filling to feed all cells



ii. Minimization of energy to pump blood from the heart to the capillaries



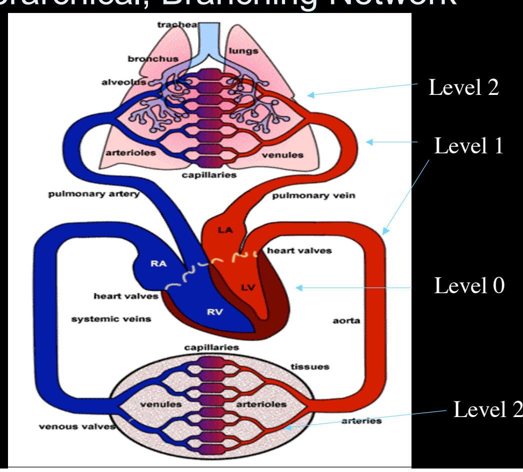
iii. Capillaries are invariant in size



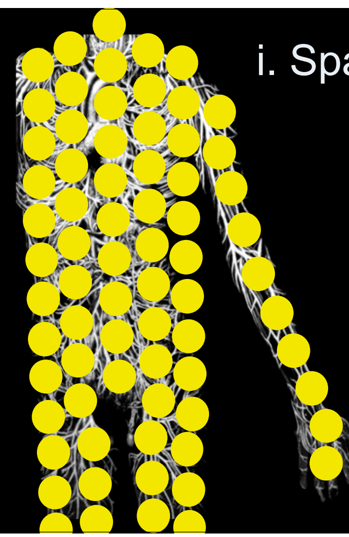
West et al. *Science* (1997)

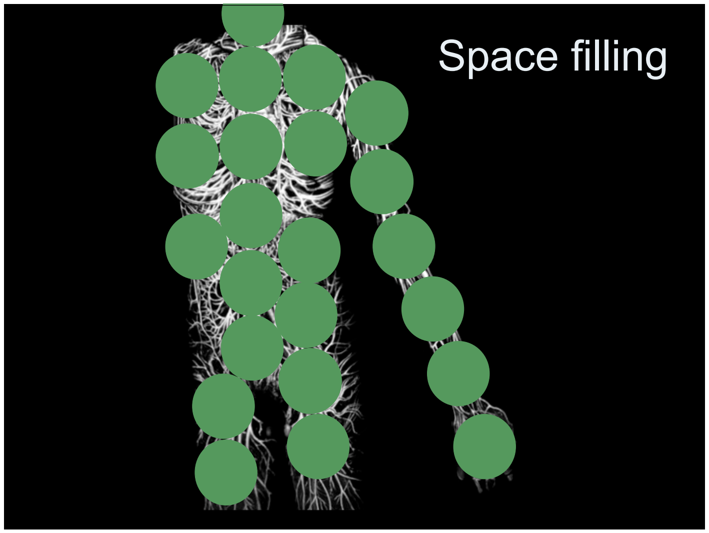
Hierarchical, Branching Network

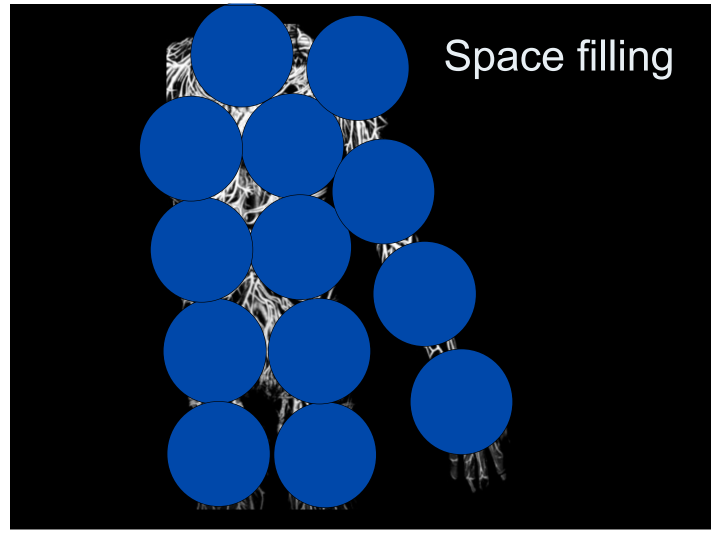
$n = 2$



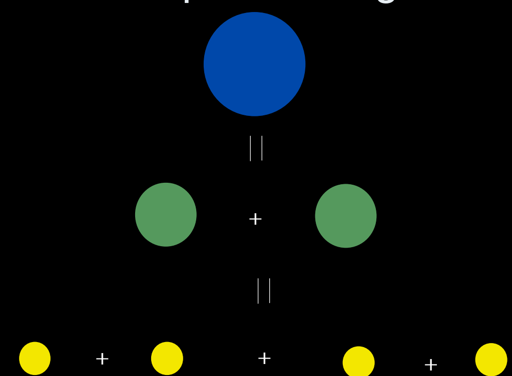
i. Space filling





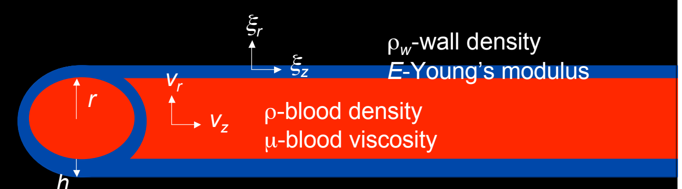


Space Filling



$$N_k C l_k^3 = N_{k+1} C l_{k+1}^3 \longrightarrow \gamma = \frac{l_{k+1}}{l_k} = \left(\frac{N_k}{N_{k+1}}\right)^{1/3} = n^{-1/3}$$

ii. Minimize energy loss through selection



Blood Flow

$$\rho \frac{\partial \mathbf{v}}{\partial t} = \mu \nabla^2 \mathbf{v} - \nabla \mathbf{p}$$

Vessel Wall

$$\rho_w \frac{\partial^2 \xi}{\partial t^2} = E \nabla^2 \xi - \nabla \mathbf{p}$$

Can derive total impedance to flow

$$Z \sim \frac{c_o \rho i}{\pi r^2} \sqrt{\frac{J_0\left(i^{3/2}\sqrt{\frac{\omega\rho}{\mu}}\, r\right)}{J_2\left(i^{3/2}\sqrt{\frac{\omega\rho}{\mu}}\, r\right)}}$$

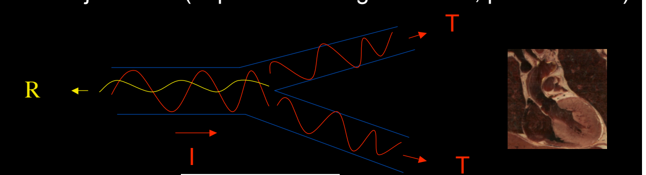
ω-angular frequency of wave

c_0-Korteweg-Moens velocity

$$c_0 = \sqrt{\frac{Eh}{2\rho r}}$$

ii. Minimize energy loss (selection)

Reflection at junctions (Important for larger vessels, pulsatile flow)

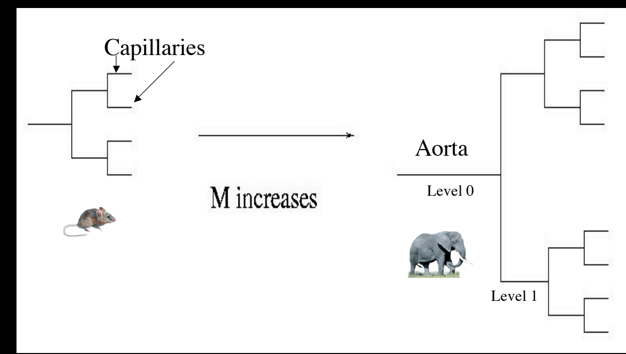


$$\beta = \frac{r_{k+1}}{r_k} = n^{-1/2}$$ Area Preserving

Dissipation (Important for small vessels, Poiseuille flow)

$$\beta = \frac{r_{k+1}}{r_k} = n^{-1/3}$$ Area Increasing

Body Size Changes Network Size



Terminal units are invariant.

Metabolic Rate, *B*, and Body Mass, *M*

$$M \propto V_b = \sum_{levels} n_k \pi r_k^2 l_k \propto N_T^{4/3} V_T \propto B^{4/3}$$

Mass

Blood volume

Number of Terminal units

Volume of Terminal units

Met Rate

Follows from Energy Min.

Use scale factors to relate each level to terminal units.

Invariance of terminal units $B = N_T B_T$

$$B \propto M^{3/4}$$

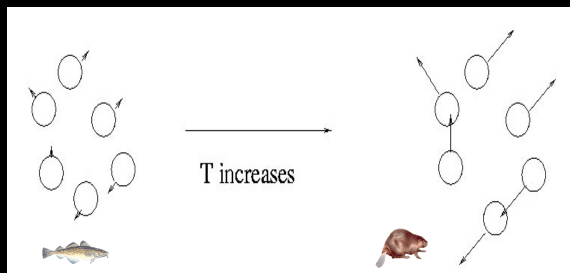
West et al. *Science* (1997)

Theory has three assumptions

- Branching, hierarchical network that is space filling to feed all cells->relates vessel lengths across levels of cardiovascular system
- Minimization of energy to send vital resources to the terminal units (pump blood from the heart to the capillaries)->relates vessel radii across levels of cardiovascular system and connects blood volume to body size
- Capillaries are invariant in size->sets overall scale for cardiovascular system

Together these determine the scaling for the network.

Theory for body temperature: biochemical reaction kinetics



Changes energy of impact and frequency of collisions,

Characteristic Biological Rates and Times

$$B = B_0 M^{3/4} e^{-E/kT}$$

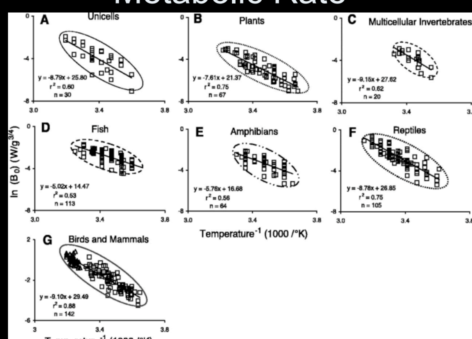
$$\overline{B} = \frac{B}{M} = B_0 M^{-1/4} e^{-E/kT}$$

$$t_{BIO} \propto M^{1/4} e^{E/kT}$$

15 orders of magnitude collapses to 1 order of magnitude variation!
Zeroeth-order model for quantifying differences between organisms and identifying other relevant parameters.

Gillooly, Charnov, West, Savage, and Brown *Nature* (2002).

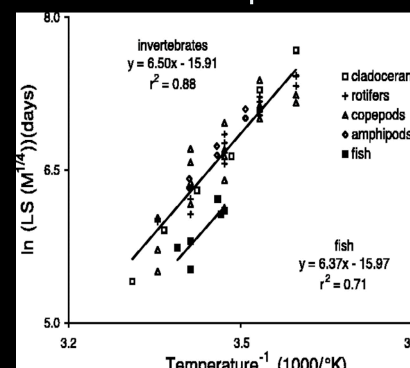
Temperature Dependence of Metabolic Rate



Similar slopes reflect similar activation energies and shared biochemistry through evolution. *M* and *T* explain dominant variation.

Gillooly, Brown, West, Savage, and Charnov *Science* (2001)

Mass and Temperature Dependence of Lifespan



Gillooly, West, Brown, Savage, and Charnov *Science* (2001)

An Anacreontick
Busy, curious, thirsty Fly,
Gently drink, and drink as I;
Freely welcome to my Cup,
Could'st thou sip, and sip it up;
Make the most of Life you may,
Life is short and wears away.

Just alike, both mine and thine,
Hasten quick to their Decline;
Thine's a Summer, mine's no more,
Though repeated to threescore;
Threescore Summers when they're gone,
Will appear as short as one.
By William Oldys

Population Level

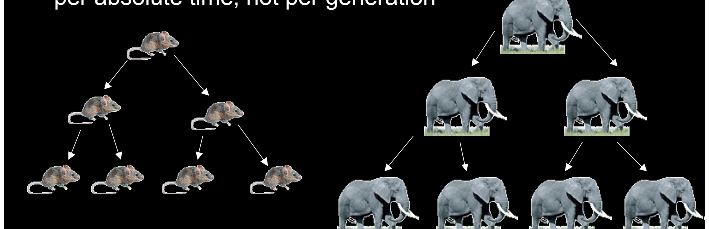
Population Growth: From Individuals To Populations

$$\frac{dN}{dt} = rN$$

or

$$N(t) = N_0 e^{rt}$$

-per absolute time, not per generation



Savage et al. *Am. Nat.* 2004

Euler's Equation (for positive growth)

-Survivorship and fecundity are also important, and can make that explicit!

$$B(t) = \int_0^\infty B(t-x)l(x)b(x)dx$$

->

$$1 = \int_0^\infty e^{-rx}l(x)b(x)dx$$

N(t) is population size at time *t*
r is rate of increase, fundamental variable
B(t) is number of births at time *t*
l(x) is probability of survivorship up to age *x*
b(x) is fecundity rate at age *x*

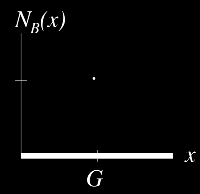
Savage et al. *Am. Nat.* 2004

Discrete Generations

Organisms reproduce once in their lifetime

$N_B(x)$ is cumulative number of offspring at age x

G is the generation time and is the average age at which an organism has offspring

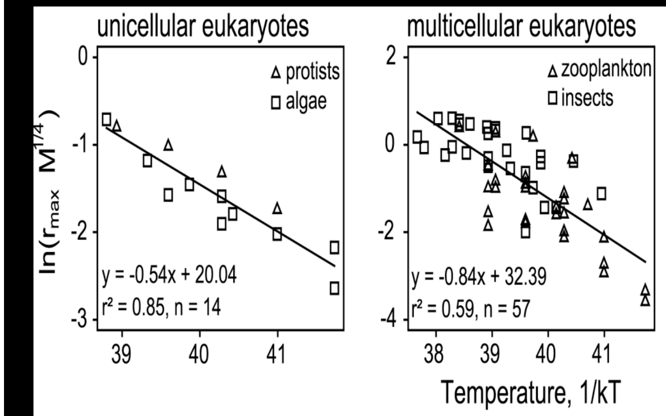


$$r = \frac{1}{G}\ln[l(G)N_B(G)] \propto M^{-1/4}e^{-E/kT}$$

Univoltine insects follow this exactly
Many other unicells, insects, and zooplankton are a good approximation to this Savage et al., *Am. Nat.*, 2004.

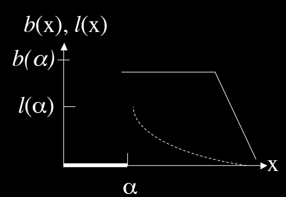
Empirical *M* dependence: Fenchel (1973), Southwood et al. (1974), May (1976), Blueweiss et al. (1978)
Empirical *T* dependence: Monod (1942), Birch (1948), Hinshelwood (1966), Droop(1968), Eppley (1972)

Intrinsic Rate of Increase



Savage et al. *Am. Nat.* 2004

Overlapping Generations



Mortality Rate

$$l(x) = l(\alpha)e^{-Z(x-\alpha)}$$

Age at 1st Reproduction

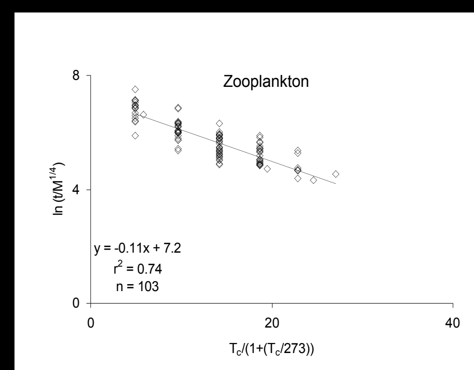
$$Z \propto r \propto \alpha^{-1} \propto M^{-1/4}e^{-E/kT}$$

$$l(\alpha) = e^{-\bar{Z}\alpha} \propto M^0 T^0$$

Size and temperature do not affect the percentage of offspring that survive to the age of first reproduction.

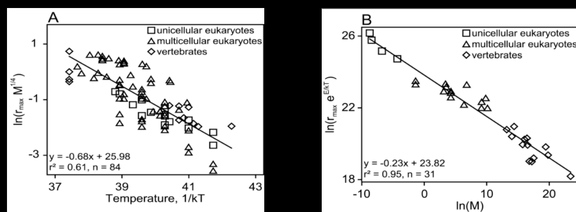
Savage et al., *Am. Nat,* 2004

Time to First Reproduction, α Measure of Development



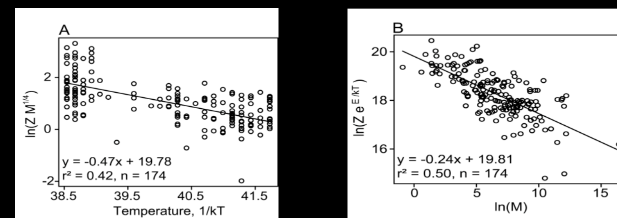
Gillooly, Charnov, West, Savage, and Brown *Nature* (2002).

Little Variation Across Broad Assortment of Organisms



Savage et al. *Am. Nat.* 2004

Mortality Rates in the Field



Data from Pauly (1980) Savage et al. *Am. Nat.* 2004

Scaling of Population Size

Assume fixed amount of resources P

At steady state, $dN/dt=0$, population is at carrying capacity for environment, $K(M,T)$

$$P \propto B(M,T)K(M,T)$$

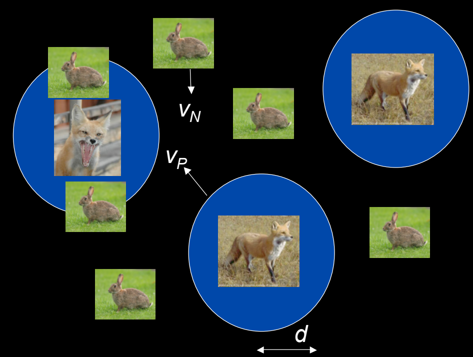
$$K(M,T) \propto \frac{1}{B(M,T)} \propto M^{-3/4} e^{E/kT}$$

With energy equivalence, Damuth, *Bio. J. Lin. Soc.* (1987), this holds for multiple populations in a shared environment

Savage et al. *Am. Nat.* 2004

Predator-Prey Interactions

Encounter Rate



Relevant Variables

Prey density---N

Predator density---*P*

Relative velocity--- $v_r = \sqrt{v_P^2 + v_N^2}$

$\sim v_P$ (fast predator, sessile prey)

$\sim v_N$ (fast prey, sessile predator)

detection distance---*d*

dimensionality---*D*

For random movement :

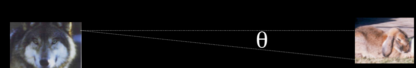
$I \propto d^{(D-1)} v_r NP$

$= 2 d v_r NP$ for D=2 (Type I linear Response)

$= 2\pi d^2 v_r NP$ for D=3

Detection Distance Scaling

$$d \propto M_P^{1/4} M_N^{1/3} T^0$$



Based on properties of eye, height, and optics of imaging as a function of size. None of these depend on temperature, so no *T* dependence. What about other senses like hearing (bats) and smell (sharks)?

McGill & Mittelbach, Evol. Ecol. Res, 2006

Velocity Scaling

Power/Mass=(Force*velocity)/Mass

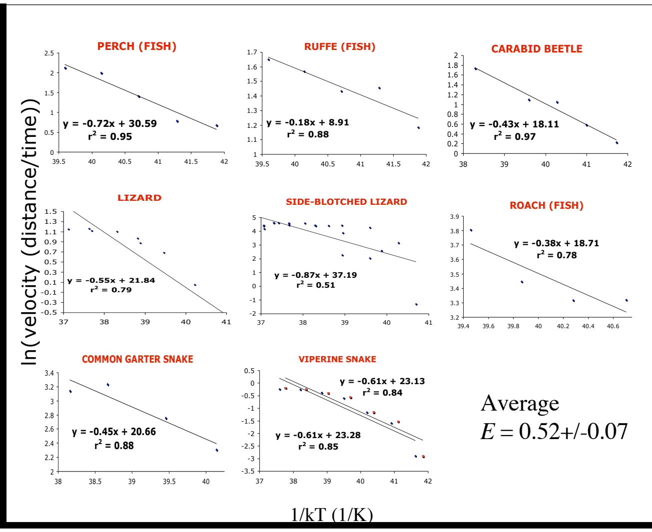
Power/Mass $\propto M^{-0.13} e^{-E/kT}$ (maximal allometry, Weibel et al., *Resp. Physiol. Neurobiol.*, 2004)

Force/Mass $\propto M^{-1/3}$ (muscle cross-section for strength and jumping, Schimdt-Nielsen, 1984)

Whence,

$$v \propto M^{0.20} e^{-E/kT}$$

Which one of predator or prey is bigger and/or warmer will likely dominate v_r. This will affect behavior of consumption rate and many other interaction and population processes.



Average
$E = 0.52$+/-0.07

Scaling depends on interaction type

-dimensionality via detection distance and thus habitat:
I. Aquatic (2D or 3D) II. Terrestrial (~2D) III. Air (3D or ~2D)

-detection distance and velocity on predator and prey strategies:
1. Active-capture 2. Sit-and-Wait 3. Gatherer

-relative velocity on relative thermy of predator-prey interaction

$$\overline{C} = IP\Pi$$

consumption rate

probability of attack

probability of success and consumption

Savage and Dell, in preparation

Consumption Rate Scaling

Depends on v_r and d, so if we now normalize by predator density and/or prey density, OR hold those densities constant (often the case in experiments), we can predict the scaling.

For example, in 2D for gatherer and often active-capture

$$\overline{C} \propto M_P^{1/2} M_N^{1/3} e^{-E_P/kT_P}$$

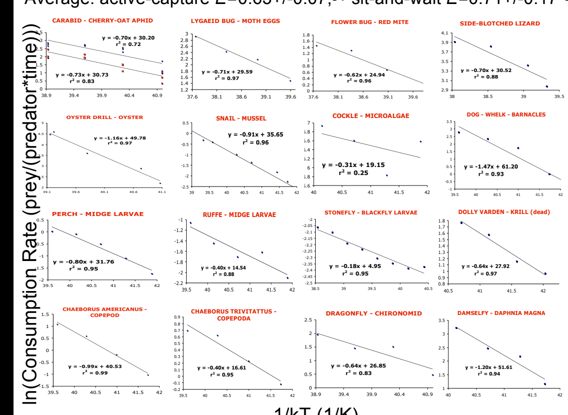
or for sit-and-wait interactions, detection distance of *prey* matters

$$\overline{C} \propto M_N^{1/2} M_P^{1/3} e^{-E_N/kT_N}$$

Savage and Dell, in

Consumption Rate Data

Average: active-capture E=0.63+/-0.07;eV sit-and-wait E=0.71+/-0.17 eV



Savage and Dell, in preparation

Predator-Prey Equations

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \overline{C}NP$$

Logistic growth with intrinsic growth, *r*, carrying capacity *K*

Death from predation

$$\frac{dP}{dt} = \varepsilon\overline{C}NP - d_M P$$

Growth from converting prey to predator with efficiency ε

Death due to intrinsic mortality scales as $d_M \propto M_P^{-1/4} e^{-E/kT}$

Weitz and Levin, *Ecol. Lett.*, 2006; Vasseur and McCann, *Am. Nat.*, 2006

Equilibrium abundances

When prey and predator population growth are zero, we have equilibrium. Scaling differs depending on conditions. For active-capture (1) and gatherer (3) with infinite prey

$$N^* = \frac{d_M}{\varepsilon\overline{C}} \propto \left(\frac{M_p}{M_N}\right) M_P^{-3/4} M_N^{-1/3} \propto T^0$$

$$P^* = \frac{r}{\overline{C}} \propto M_P^{-1/2} M_N^{-1/4} \left(\frac{e^{-E_N/kT_N}}{e^{-E_P/kT_P}}\right)$$

Also predict coexistence curves (what eats what), strategy used by predator, cycling times for booms and busts

Physics [Science] is mathematical not because we know so much about the physical world, but because we know so little; it is only its mathematical properties that we can discover.
~Bertrand Russell

Conclusions

1. Power laws are common in biology (and elsewhere)

2. Dynamical model based on distribution of resources makes many predictions that match data.

3. Temperature also affects biological rates and times and can include this effect

4. Can build up from one level to the next to understand population growth (but ants…)

5. Species interactions and competition can begin to be incorporated into both scaling and models of effects of climate change on biological systems.

Collaborators

Geoff West (Santa Fe Institute and Los Alamos)
James Brown (U of New Mexico)
James Gillooly (U of New Mexico)
Woody Woodruff (Los Alamos)
Drew Allen (U of New Mexico)
Eric Charnov (U of New Mexico)
Alex Herman (UC San Francisco)
Tony Dell (James Cook University)
Jon Norberg (Stockholm University)
Colleen Webb (Colorado State University)
Eric Deeds (Harvard Medical School)