

### Lecture 3: Acquiring and allocating resources/ constraints & trade-offs

#### Outline:

Tolerance limits

Limiting factors

Regulation vs. Limitation

Limiting factors - *never* just one

Energy is a broad limiting factor.

Factors affecting energy requirements

Endothermic/Ectothermic heat *production*

Homeothermic/Poikilothermic heat *regulation*

Body size - surface:volume ratios

Methods of movement

Trophic level and assimilation efficiency

Time and energy budgets

↑ in foraging time ⇒ ↑ in available energy

↑ in foraging time ⇒ ↓ in time available for other activities

problem of common currency - energy, time, fitness

Principle of Allocation (of resources/energy/time)

Growth, maintenance, reproduction

Utilization curves and trade offs in efficiency - generalists vs. specialists

Design constraints & trade offs

Example: heat regulation

Turn on, tune in, drop out

Adaptive suites

From Lect.1 - Geographic distributions of *species* are determined in part by temperature and precipitation. (Fig. 2.3 Begon et al.)

At *individual* level, can see the mechanisms (behavioral, physiological, demographic) that produce species distributions, using **tolerance curves**. Tolerance curves relate tolerance or performance to environmental variation.

Examples with *behavioral* response variables:

- (1) Swimming speed of goldfish vs (water) temperature. Slow swimming  $\Rightarrow$  less food *and* more vulnerable to predation (Fig 5.8 Pianka)
- (2) Jumping distance vs (body) temperature in frogs (Fig 5.2 Pianka)

Examples with *physiological* response variables:

- (3) Arthropod 'state' vs temperature (Fig 2.1b Begon et al.)
- (4) CO<sub>2</sub> uptake vs temperature in *Atriplex* leaves (Fig. 5.8b Pianka)

Example with *demographic* response variable:

- (5) Shrimp mortality vs temperature and salinity (Fig 2.27b Begon et al.)

The last example plots tolerance (measured by survival) against 2 environmental variables, rather than one. In real world, animals operate w.r.t many variables. (Fig 2.26 Begon et al.)

By affecting behavior, physiology (ultimately affecting survival and reproduction), ecological factors (all abiotic above, but can also be biotic, e.g. competitors or predators) limit distribution and numbers.

**Limiting factor** is any factor that reduces survival or reproduction within a population.

Terminology: **Limitation**  $\equiv$  tending to reduce numbers (reduce survival or reproduction)  
**Regulation**  $\equiv$  tending to hold numbers constant

Caveats:

- (1) Common to speak of food-limited or predator-limited populations, but there is *never* just one limiting factor for a population.
- (2) Limiting factors may **interact**, with factor A modifying the impact of factor B. E.g. from African wild dogs with interspecific competition and viral diseases. (Figs. from Cons Biol and JWD papers).

(3) For some populations, there might be a **master (dominant) limiting factor**, which has impact substantially greater than other factors. More likely in disturbed ecosystems, where impacts of some factors (e.g. predation, fire) have been eliminated/reduced

**Energy** is a limiting factor important for most animals.

In thermodynamic terms, animals are open steady state systems, meaning that they require external input of energy to maintain constant internal conditions (homeostatis  $\equiv$  'same state'). In great majority of animals, there is a narrow range of internal conditions (temperature, pH) within which physiology can function. If denied sufficient energy, homeostasis is not maintained and animal dies.

**Energy requirements** affected by:

(1) **Source of body heat.**

**Endotherms** produce their heat by metabolic oxidation.

**Ectotherms** derive heat directly from environment, by absorption of solar radiation, or by regular source/sink conduction from air, ground, water.

Endotherms > ectotherms w.r.t energy required/ kg of body mass

(2) **Method of body temperature regulation.**

**Homeotherms** (thermoregulators) maintain ~ constant internal temperature.

**Poikilotherms** (thermoconformers) allow fluctuation over wide range in  $\updownarrow$  with environment.

Homeotherm > poikilotherm w.r.t energy required/ kg of body mass

Example of thermoregulator and thermoconformer: Charles Blagden who roasted himself for 45 minutes at 265°F and survived. He thermoregulated. The steak he took into the oven thermoconformed and was cooked to a crisp! (This was supposedly published in the Philosophical Transactions of the Royal Society of London, a prestigious journal. I've never been able to find the paper, but the reference is Blagden, C. 1775. Experiments and observations in a heated room. Phil Trans Roy Soc Lond 65:111-123. )

(Fig. 5.10 Pianka)

Note that conforming  $\rightarrow$  regulating is a *continuum*. E.g. cats almost complete regulator, lizards almost complete conformer, most species fall in between

(Fig. 16-18 Eckert)

Even within body areas of a given individual there is variation in degree to which temperature conforms to environment or is regulated. Regulate critical areas more closely, let extremities go - this is why you get frostbite first in toes and fingers.

(Figure 16-30 Eckert)

**(3) Body Size** - energy needed *per unit of body mass* decreases as body size increases

Assume animal is spherical with radius =  $r$

$$\text{Surface} = 4\pi r^2$$

$$\text{Volume} = \frac{4}{3}\pi r^3$$

$$S/V = 3/r \quad \text{equivalently} \quad S = aV^{0.67} \quad (\text{where } a = \text{coefficient that varies among taxonomic groups depending on shape})$$

In words, as size (radius)  $\uparrow$ , S/V ratio  $\downarrow$ . Compare a sphere of with  $r = 1\text{mm}$  (water flea) to a sphere with  $r = 100\text{mm}$  (black bear). S/V is 100 times greater for the flea. S/V ratio declines as radius increases.

Small body  $\Rightarrow$  high S/V ratio  $\Rightarrow$  high rate of heat loss to environment  $\Rightarrow$  high energy requirement per unit of body mass.

Animals are not actually spheres, so the empirical relationship has exponent of  $\sim 0.63$ , close to expected 0.67 but not identical.

(Fig 16.7 Eckert)

Empirical relationship between energetic requirements (metabolic rate) and body mass is similar to S/V relationship :

$$\text{Met. Rate} = a * \text{body mass}^{0.67 \text{ to } 0.75}, \quad \text{similar to the S/V equation.}$$

(Fig. 5.10 Pianka) (Fig 5.12 Ricklefs)

True for different size *individuals* within a species, also.

(Fig 16.8 Randall)

**4. Method of movement.** Energy needed for:

Running > Flying > Swimming > Sessile,

due to differences in friction, costs of overcoming gravity, and biomechanics.

Interaction between method of movement and size: (as with S/V) lower energy requirements for larger animals, within a type of locomotion.

(Fig. 3.22 Gordon, 16-43 Eckert)

Reynolds Number,  $R_e = \rho VL/\mu$

$\rho$  = density of medium

$\mu$  = viscosity of medium

V = velocity

L = length (or other measure of size) of animal

When  $R_e < 1$ , pure laminar flow

$R_e > 40$  turbulent wake

$R_e > 10^6$  (1 million) turbulence passing over body (stall!)

*small* animals: V & L small &  $\mu$  large: movement constrained by *viscosity*

*large* animals: V & L large &  $\mu$  small: movement constrained by  
*turbulence, a weaker constraint*

### 5. Trophic level and assimilation efficiency

Some terminology: (Figure 11.10 Ricklefs)

Ingestion = assimilation + egestion + excretion

Assimilation = productivity + respiration

Productivity = growth + reproduction

Assimilation efficiency = energy assimilated/energy ingested

Low for herbivores (which convert plant  $\Rightarrow$  animal and must deal  
with cellulose, alkaloids, etc)

High for carnivores (which convert animal  $\Rightarrow$  animal)

### *Time and energy budgets.*

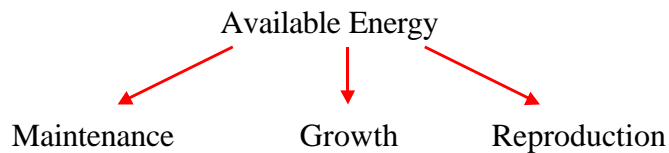
Energy commonly is limiting.

But as long as benefits of foraging exceed costs, an animal could get more energy simply by increasing foraging time.

↑ in foraging time ⇒ ↑ in energy available.... but  
↑ in foraging time ⇒ ↓ in time available for other activities (territorial behavior, mate acquisition, predator avoidance, etc.)

The goal is to balance these relationships to maximize *fitness*. In general, we have little empirical data on how time in various activities and energy intake relate to fitness.

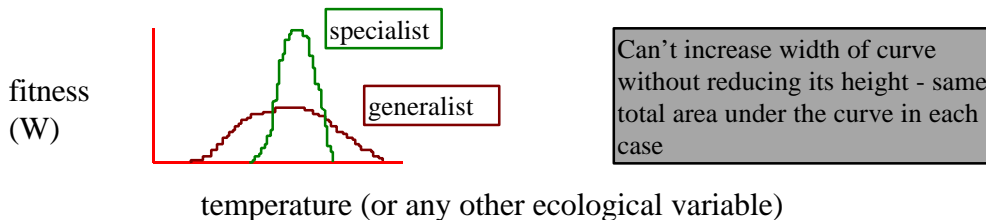
The idea of trade offs leads to... **Principle of Allocation**, which simply states that available energy must be allocated to one of three basic processes:



↑ in one process ⇒ ↓ in others - there are *trade-offs* among M,G,R and the goal is to allocate energy to each in a way that, over lifetime, maximizes fitness. This will be seen later in *life-history evolution*.

E.g. young animals allocate heavily to G, zero to R.  
*Iteroparous* species allocate some energy to R every year, while *semelparous* species wait, breed once, die (e.g. salmon).

Similarly, trade-offs apply to the classification of animals as *specialists* or *generalists*.



### **Design Constraints & Adaptive Suites**

Animal must be adapted w.r.t many different variables.

*Design constraints*: Improvement on one axis can affect the choices along another axis.

E.g. ↓ body size ⇒ ↓ in total energy required, but ↑ vulnerability to predators  
↑ foraging time ⇒ ↑ net energy, but ↑ vulnerability to predation.

*Adaptive suite*: a set of co-adapted traits that work well (give high fitness) in combination

Example: tooth morphology, depth of foraging and major prey types in seals (Fig. 1.18 Ricklefs)



*Temperature regulation in desert adapted species*

Pathways of heat gain & loss are:

Radiation, Conduction, Convection, Evaporation

(Fig 5.17 Pianka)

Diferent species use diferent sets of traits (behavioral, morphological, physiological) to solve problem of living in extreme heat with little water.

Strategies used depend (not surpisingly) on body size:

*Kangaroo Rat*: “Turn on” strategy of thermoregulation.

- small size  $\Rightarrow$  high S/V  $\Rightarrow$  problem w/temperature regulation
- try to minimize H<sub>2</sub>O loss: no sweat glands
- this creates problem with water
- ultra-efficient kidney - long loops of Henle - urine saltier than sea-water (salt concentration =24% compared with 6% in man)
- countercurrent circulation in nose cools exiting air to 28°C, compared with 38°C body temp (cool air holds less water)
- nocturnal, deep den

*Camel* - “Tune in” strategy of thermoconforming when H<sub>2</sub>O limited

- large  $\Rightarrow$  low S/V  $\Rightarrow$  reduces problems of temperature regulation
- can lose up to 17% of body mass (30% of body water) due to water loss to regulate evaporatively. This is 2x the loss that would kill most mammals (10% loss of body water causes kidney failure in man).
- If water available, thermoregulates. Can drink 25-30% of its weight in one drink. 1 gal/min for 25 minutes!
- can tolerate high body temperature: once body temp approaches environmental temp, no longer keep gaining heat. Then ‘dumps’ heat at night, by passive conduction/radiation. If lacking water, thermoconforms.
- but only *short-term*: if camel cannot reach cooler conditions to lose heat by radiation and replenish water lost to evaporation, it dies

*Mohave Ground Squirrel* - “Drop out” strategy

- allows temperature to go up in short burst of activity
- then returns to burrow and re-radiates heat
- this avoids water problems, but must deal with sporadic activity budget - limited time for foraging, territorial defense, mate search, etc.
- when conditions are too dry, aestivates. Torpid; metabolic rate drops to  $\frac{1}{6}$  of normal; temperature tracks environment and water loss is greatly reduced.