Optimal foraging

1) Optimization approach
2) Optimal diet in a predator
3) Optimal foraging in plants
4) Habitat selection
5) The foraging gain predation-risk tradeoff
6) Example exam questions
1) Optimization approach

Rather than ask:
   What do consumers eat? Where do they feed?

Ask instead:
   What should they be eating? Where should they feed?

Base the inquiry on the principle that natural selection acts on populations so as to result in strategies (phenotypes) that maximize expected gain while foraging.

This doesn’t imply that natural selection is expected to produce the best conceivable phenotype.

Instead, natural selection is expected to result in the best phenotype given the constraints (not always specified).

The currency that is maximized by selection is fitness, but to be useful a more direct performance measure is conceived: growth rate, or energy gain while foraging.
2) Optimal diet in a predator

Field inaugurated by MacArthur & Pianka (1966)

They asked: What should a predator eat?

Assume:

- Predator encounters prey items randomly in proportion to their abundance
- Predator maximizes energy gain per unit time
- Prey items are of equal energy content but vary in their handling time
- Items are identical in nutritional content (e.g., predator is a carnivore)
- Cost of foraging is time, which is spent searching and handling
2) Optimal diet in a predator

Simple predictions:

1) Predators should always include the most profitable items in the diet, no matter how rare.

2) Whether or not a prey item type is included in the diet does not depend on its abundance, but only on the abundance of items of higher value.

3) As food abundance declines uniformly, the number of prey item types in the diet should increase.
2) Optimal diet in a predator

Test of optimal diet in shore crabs


http://massbay.mit.edu/exoticspecies/exoticmaps-descriptions_intro.html
Photo: P. Erickson
2) Optimal diet in a predator

Test of optimal diet in great tit

Krebs et al. (1977) Animal Behavior

http://commons.wikimedia.org/wiki/File:Great_Tit_(Parus_major)_1.jpg
3) Optimal foraging in plants

Plants ‘behave’ by redirecting growth.

Resources types are non-substitutable and essential (e.g., light & nutrients).

Resource types are often harvested with different tissues (shoots vs roots).

Growth of plant is limited by the most limiting resource.

How should a plant best allocate resources to roots and shoots so as to maximize growth rate?

3) Optimal foraging in plants

Theoretical prediction:

A plant should adjust allocation so that, for a given expenditure in acquiring each resource, it achieves the same growth response.

At this point, growth is equally limited by all resources

Bloom et al. (1985); Tilman (1988)
3) Optimal foraging in plants

Meta-analysis: tests of optimal allocation in plants

LMF: leaf mass fraction
SMF: stem mass fraction
RMF: root mass fraction

Fig. 6. Difference in biomass allocation between plants grown at a high and a low level of resource availability. Average values (± s.d.) for a wide range of plant species and experiments. (A) Experiments that varied irradiance (130 observations in 40 publications). (B) Experiments that varied CO₂ partial pressure (n = 170 in 80 publications). (C) Experiments that varied nutrient availability (n = 150 in 60 publications). (D) Experiments that varied water availability (n = 70 in 30 publications). Asterisks at the bottom of the panels indicate the significance level under the H₀ hypothesis of no difference in allocation, combining the data for herbs (grey bars) and woody plants (open bars). *, P < 0.05; **, P < 0.01; ***, P < 0.001.
4) Habitat selection

Test of optimal habitat selection in bluegill sunfish

1. Developed an optimal diet model
   \[
   \text{Max}(E/T) = \frac{(E_{\text{gain}} - E_{\text{loss}})}{(T_S + T_H)}
   \]

2. Measured the handling times for natural prey as a function of prey and sunfish size

   Feeding on sediment prey results in the highest handling time (fish actually engulfs a mouthful of sediment and then sieves the prey in the mouth before swallowing)

http://io.uwinnipeg.ca/~simmons/16cm05/1116/16behave.htm
4) Habitat selection

3. Measured search times (prey encounter rates) of fish feeding in the three main habitats as a function of prey density.

Prey encounter rates were higher for higher prey densities, larger prey and larger fish (which are known to have higher visual acuity and sensitivity).

---

**Fig. 2.** Representative examples of laboratory prey encounter rates (\( \bar{x} \pm 1 \text{ SE} \)) in relation to prey density, prey length and fish length. Results shown in the first panel are from two 65-mm bluegills feeding on *Daphnia* (1.14-mm body length). The second panel shows results from two 110-mm bluegills feeding on Coenagrionidae (192 naiads/m\(^2\)) and the third panel shows data from eight bluegills feeding on 11.1-mm *Chironomus* larvae at 1000 larvae/m\(^2\). Curves were fitted by the regression equations in Table 4.
4) Habitat selection

4. Measured density and prey sizes in a natural lake in the three different habitats.

5. Used the model to predict what the optimal prey size would be for each fish size in each habitat.

6. Checked that the model did a good job predicting the diets of fish. It did!
4) Habitat selection

**Fig. 7.** Seasonal pattern in predicted habitat profitability (left) and actual habitat use (right) for three size classes of bluegills. Actual habitat use determined from the mean amount of prey (milligrams dry mass) foraged from each habitat. Dashed lines and closed circles represent the open water, solid lines and closed circles the vegetation, and dotted lines and open circles the sediments. Sample sizes were 3-5 fish/date for large bluegills (101-150 mm), 5-9 fish/date for medium bluegills (51-100 mm) and 4-9 fish/date for small bluegills (10-50 mm).

4) Habitat selection

5) The foraging gain - predation risk tradeoff

Fig. 1. Apparatus used for experiments 1 and 2. Food is provided by feeders (A) located on either side of the screen (B). The feeder on the right could be placed 2, 16, or 32 cm from the screen. The mesh size of the screen restricted the predator (C) to the right side of the aquarium while allowing the guppies to move freely between sides.

5) The foraging gain - predation risk tradeoff

An hypothesis that incorporates mortality into habitat selection model

Fig. 11. (a) Hypothetical growth (g) and daily mortality (µ) rates as a function of bluegill size in the vegetation (v) and pelagic (open-water, o) habitats. (b) Ratios of µ/g for the pelagic and vegetation habitats for the curves in panel (a), illustrating the prediction of two switch points in the bluegill life history, i.e., from the pelagic habitat to the vegetation and then back to the pelagic.
6) Example exam questions

In a fine grained environment, should a uniform reduction in food abundance cause an optimal forager to become more selective or less selective in their choice of diet? Why?

Should animals minimize their risk of mortality from predation while foraging? Why or why not?

How should a plant allocate resources to roots and shoots so as to maximize growth rate?

If individual plants are experimentally provided with more light, how should this affect their allocation of resources to leaves and roots? Why?

Imagine that there are two habitats available to a foraging juvenile sunfish. Habitat A has more food than habitat B, but it also has a higher risk of predation. The ratio of predation risk to foraging gain in the two habitats, $\mu/g$, is the same. Should the sunfish prefer habitat A, habitat B, or be indifferent? Explain.