Lecture 4: Foraging tactics and optimal foraging models

Outline:

Foraging Tactics
- Cropping
- Active hunting
- Sit-and-wait hunting

Scale of habitat and habitat use
- Fine-grained
- Course-grained

Optimality
- Patch model
- Prey model
- Risk sensitive foraging
- Z-score model

Foraging Tactics: three major tactics, use depends on trophic level and characteristics of food type. Cropper, active hunter, sit-and-wait hunter

Croppers (most common)
- utilize a dense food supply
- time and energy allocated to ingesting and digesting
- less effort in search/capture
- high quantity of low quality (energy assimilated per kg) food
- herbivores, filter feeders

Active Hunters (less common)
- utilize food that is low density, patchy, or difficult to catch
- time and energy allocated to search and capture
- less effort in ingestion and digestion
- low quantity of high quality food
- mammalian carnivores, frugivorous primates

(Figure 15-14 Eckert)

Sit-and-wait hunter (least common)
- utilize dense, mobile food
- little energy into *any* component of foraging, but capture and digestion highest
- very low quantity of high quality food, offset by very low costs compared to croppers and active hunters

- some predatory fish, antlions, web spiders (note - often modify environment to create trap)

Scale of Habitat Use

Terms fine-grained or course grained are widely used, in two ways:

Habitat:

fine-grained ≡ uniform on the scale of forager's movements
course-grained ≡ patchy on the scale of forager' movements

Utilization patterns:

fine-grained ≡ animal uses resources in proportion to their occurrence in the environment
course-grained ≡ animal uses resources in a patchy way ; some resource types used more than proportional to abundance; some types less

Optimal Foraging Models.

One of the best developed areas of ecology in terms of theory.
Many models exist with currency = ***net rate of energy intake***.
Models analyze a behavioral decision to maximize net rate of intake (e.g. stay in current patch and keep eating vs. search for new patch) (hunt the prey encountered, or skip it and search for other prey).

Patch Selection Model ≡ Marginal Value Theorem (Charnov 1976)

Model of choosing *residence time* in a patch of food, for an animal that forages by alternately searching for a food patch or eating within a patch.

Assumptions:

(1) Maximize long-term rate of energy intake ⇒ max fitness.

(2) Resources are patchy (clumped, under-dispersed), on spatial scale of forager movements. A given food may be regular for one species and patchy for another. E.g. grove of fruiting trees relative to a fruit fly (regular) and a bear (patchy).

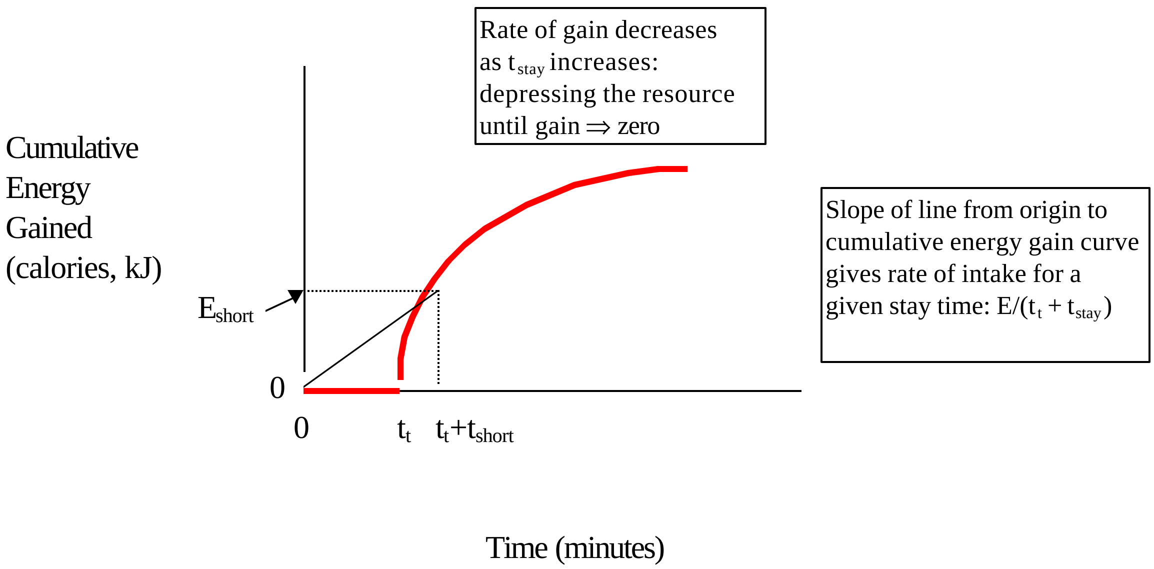
(3) Feeding in a patch and searching for a new patch are mutually exclusive.

(4) Patches are encountered sequentially (not simultaneously) when searching, with random variation around a mean search time. (I.e. model not applicable to choosing among two patches available at once).

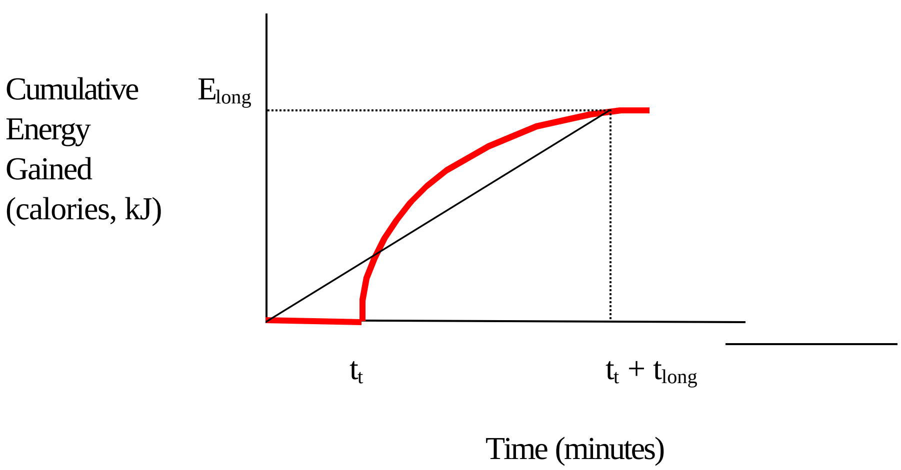
(5) Animal behaves as though it ***knows*** the average patch quality (food availability) in environment, and can instantaneously assess the food availability for patch it is in (This can be due to *genetically*-determined threshold, a *rule of thumb,* or *active observation*.)

Model: ***Decision variable*** = time in patch

At time 0, animal begins search. After average travel time t_t, encounters a patch

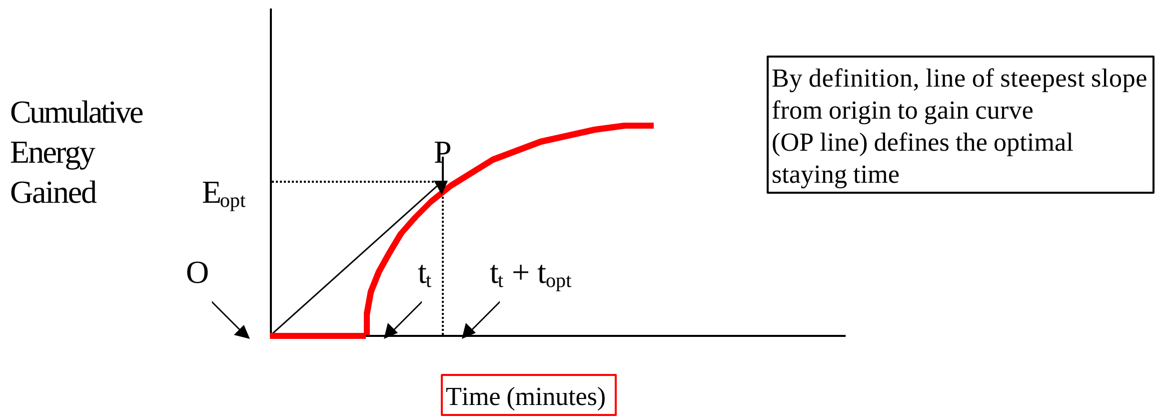


Short stay: Energy intake rate = $E_{short}/(t_t + t_{short})$



Long stay: Energy intake rate $E_{long}/(t_t + t_{long})$

To determine optimal stay:



Stay too short ⇒ waste time in travel between patches, with gain rate = 0 while traveling
Stay too long ⇒ intake rate drops as patch is depleted
Optimal stay ⇒ balances effects of depletion and travel costs.

Model Predicts Fig 9.16 Begon et al):

1. Leave ***ALL*** patches (good or bad) when the rate of gain is equal to the slope of the steepest line from origin to curve. Leave very poor patches (with slope < OP line) immediately, w/o eating

2. Patches should be abandoned more quickly when travel time between patches is short.

3. Patches should be abandoned more quickly when overall productivity is high than when it is low.

Tests of model:

Prediction 1: Hubbard & Cook (1978), parasitoid wasps, *Venturia,* depart good and bad patches at same rate of gain, as predicted. (Fig 9.18 Begon et al)

Prediction 2: Cowie (1977) Great tits, *Parus*, foraging in sawdust filled cups. Tightness of lid = travel time. As travel time ↓, time in patch ↓, as predicted. (Fig 9.17 Begon et al)

Prediction 3: Kacelnik (1984) experimentally varied mean patch quality (beetle larvae) for starlings gathering food for nestlings ⇒ more persistent within a food patch when overall food availability is low, as predicted.

Prey Model (MacArthur & Pianka 1966, Charnov 1976)

Model examines decision of what prey types to include in diet. I.e, examines decision whether or not to attack a prey type upon encounter.

Assumptions: (note similarities to patch model)

(1) Maximize long-term rate of energy intake ⇒ max fitness.

(2) Searching for prey and handling prey (catch, kill & eat) are mutually exclusive.

(3) Prey are encountered sequentially (don't encounter two types at once) at random.

(4) Energetic value of prey (e_i) handling time (h_i) and search time (s_i) are constant for each prey type.

(5) Complete information

Model: ***decision variable*** = probability of attacking prey of each type

For each prey type, measure:

e_i = energy gained by killing individual prey of type *i*
h_i = handling time for prey of type *i* (catch + kill + eat)
s_i = mean search time for prey of type *i*

Rank prey by from most to least profitable:

Profitability = e_i / h_i

Starting with most profitable prey, add prey types to the diet as long as:

$e_i / h_i \quad \bar{e} / (\bar{s} + \bar{h})$

Model Predictions:

1. Searchers (s is big & h is small) should be generalists, taking many prey types. If handling time is low relative to search time, the animal can barely begin a new search in time needed to handle current prey.

2. Active predators (h is big and s is small) should be specialists. Handling time (and effort) is great, while prey are easy to find (search times short). Thus, ignore abundance of prey types (*s*) and focus decision on profitability (take only prey for which *e/h* high).

3. For unprofitable prey, abundance is irrelevant. If e_i/h_i is less than threshold for equation, it simply doesn't matter how often the prey is encountered, it does not pay to eat it.

4. A predator should generalize when environment is unproductive, and specialize when environment is productive. As productivity ↓, s↑. Large s in denominator of equation RHS, means lower e_i/h_i satisfies criterion for inclusion in diet

Tests of Model:

Prediction 1: Insectivorous birds in trees have long search times and are generalists - take essentially all of the tiny, quickly handled insects they encounter.

Prediction 2: Most large carnivores focus on 1 or 2 of the prey species available. Yellowstone wolves >75% elk diet.

(overheads: AWD example - model predicts diet well (weak test)
model does not predict attack probabilities (strong test)
reasons for lack of fit - injury not incorporated

Prediction 3: Often not supported by data - many studies show that unprofitable prey are eaten at some low rate, not ignored completely. Possible due to violation of assumption about constant e, h, s - maybe take particularly vulnerable or profitable *individuals* of given type.

(overheads: AWD example)

Prediction 4: Bluegills and great tits both specialize when environment is rich, generalize when environment is food poor. (Fig. 9.3 Begon et al.)

Risk Sensitive Prey Models (Caraco 1980)

Both the patch model and the prey model are based on ***mean*** rate of energy intake - don't take ***variance*** into account.

Example: Choose between two hunting strategies.

Strategy A ⇒ 6 kg /day, every time. Mean = 6, variance = 0
Strategy B ⇒ 3 kg/day half of the days, 7 kg/day other half. Mean = 5, variance <> 0

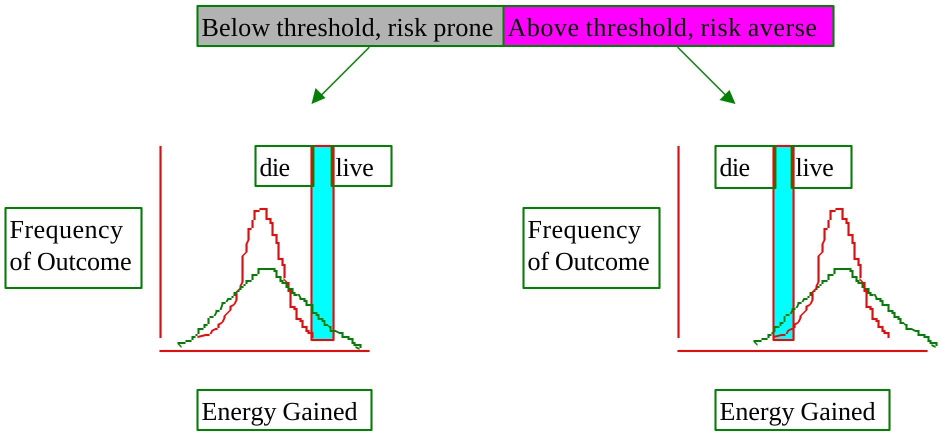
requirements = 7 kg/day

Strategy A = sure death
Strategy B = reasonable chance of survival (in the short run)

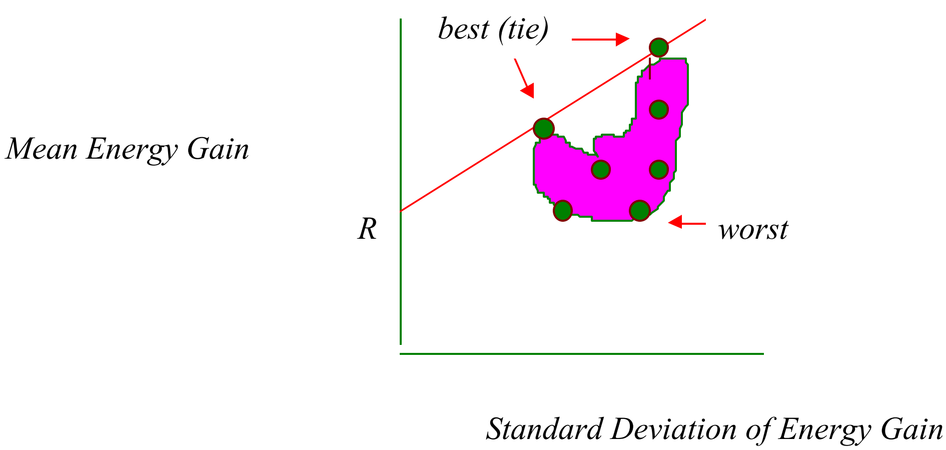
Even though ***mean intake*** is higher for A than for B. The mean alone does not predict the risk of starvation, the optimal strategy depends on ***variance*** in intake also.

Below the threshold of starvation, animals will become ***risk-prone***:
favor strategies or prey types with ***high variance*** (for given mean), to give some chance (albeit small) of getting above starvation threshold. Desperate measures in desperate times.

Above the threshold of starvation, animals will be ***risk-averse:***
favor strategies or prey type with ***low variance*** (for given mean), to minimize the risk of dropping below threshold.



Z-Scores Model (Stephens & Charnov 1982, Stephens & Krebs 1986) applies risk sensitive foraging ideas to rank prey items in rank that minimizes risk of falling below requirements.



The steepest line from requirements to mean/variance point within prey set defines the prey type that minimizes chance of dropping below requirements.

Overheads: Lions (Scheel 1991)
AWD