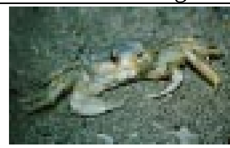
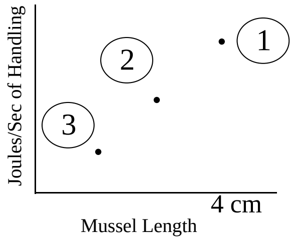
Evidence from the field:

Shore Crabs and Mussels

Elner and Hughes 1978



- Shore Crabs forage for mussels which come in different lengths.
- Different length mussels provide different amounts of energy per second of handling time.
- Elner and Hughes collected mussels of 3 different sizes and measured crab energy gain.



- 3 size classes in rank order of energy gain per unit of handling time. 1, 2, and 3.
- <u>The Manipulation</u>: Fix the proportion of different sized mussels but vary the overall abundance (# of each class in a given area).
- <u>The Observation</u>: Proportion of each size class eaten under different abundances.

Size Class--->	1	2	3
Low Abundance (Available)	*2*	*4*	*8*
Low Abundance (Eaten)	*30%*	*65%*	*5%*
High Abundance (Available)	10	20	40
High Abundance (Eaten)	60%	35%	5%

- <u>The Conclusion</u>: The crabs are foraging in a size-selective manner AND they get more selective at higher abundances.
- Note though, they still sample unprofitable size classes.

Crabs behave somewhat as one would expect:

Comparing to "coin-foraging"

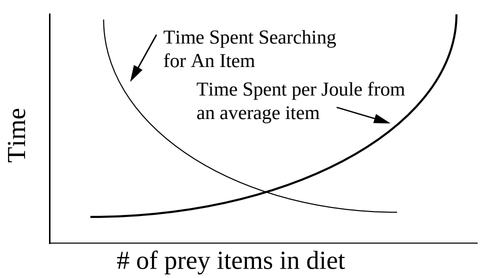
- Our foraging experiment with pennies, nickels, dimes, and quarters was similar:
- The handling times for each coin type were equal, but the "energy-gains" followed the value of the coins.
  - Different gain/time values for different coins
- Under high abundance, participants could be more selective for high-value coins, even when there were many more pennies to be found.

- This phenomenon can be predicted by the graphical analysis we did relating to MacArthur and Pianka's diet breadth model.

A tidy graphical result:

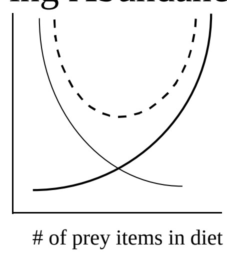
MacArthur and Pianka revisited

- Thinking in terms of crabs and mussels:
  - Searching and handling are mutually exclusive
  - Call different mussel lengths the "prey types"
  - Energy per handling time greatest by specializing on size class 1. And decreased when more size classes are added.
  - This is equivalent to noting that handling time per unit energy increases when more size classes are added to the diet.

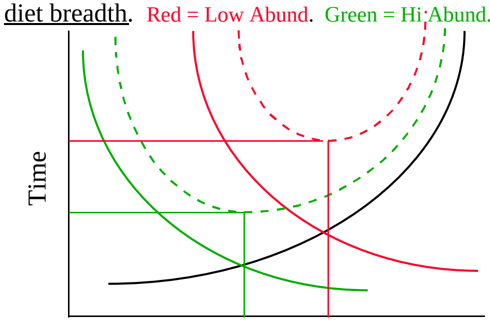


The Effect of Δ-ing Abundance

- The goal of the optimal foager is to minimize time per energy yield which is the dotted line to the right:



<u>• Increasing the abundance shifts the search time curve down and to the left--decreasing optimal diet breadth</u>. Red = Low Abund. Green = Hi Abund.



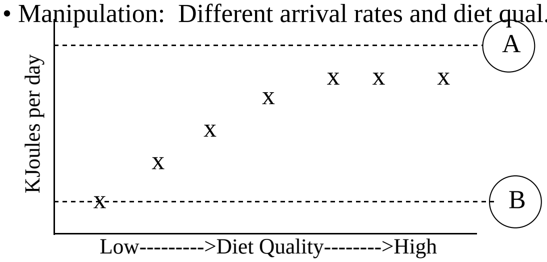
A further experiment:

Brown Trout Prey Selection

Ringler (1979)

Prey Classes:
- Brine Shrimp (15 Joules)
- Small Crickets and Mealworms (104 J)
- Large Crickets and M-worms (230-240 J)

- Aquatic "Conveyor Belt" for food
  - Expmter can manipulate "search times"
  - Fish can't handle two prey items simultaneously
- Manipulation: Different arrival rates and diet qual.



A = Optimum predicted on highest quality diet
B = Optimum predicted on low quality diet (only brine shrimp)

- Brown trout never achieved their optimal energy intake at the high quality diet, because they kept sampling the lower quality brine shrimp (and hence missed some high quality food oppotunities.
- Why? Look back at assumptions:
  - Maybe trout can't rank prey quality
    - Perhaps more learning of rank quality is needed
  - "Ambient Background Sampling" may be advantageous if novel prey types appear or if handling times can be decreased through learning:
    - Morgan 1972 with Dog Whelks eating a novel mussel variety. Over 60 days handling time per mussel decreased threefold.
  - Currency assumptions may be wrong---maybe energy isn't the limiting factor.
- There are quite a number of models that try to account for such factors--->complicated mathematics.
- Maybe there are too many constraints/ complexities for evolution to produce optimally feeding trout.

Seabirds and shell-breaking:

Revision of Optimality Hypotheses---Examples

- Three Examples:
  - NW Crows and Whelks
  - NW Crows and Mussels
  - Oystercatchers and Mussels
- Encapsulate the Adaptationist reply to criticism from non-Adaptationists
- Demonstrate what is deemed relevant to the optimal foraging modeler:
  - Finding plausible explanations for behavior
  - <u>Not</u> trying to prove that evolution has made everything the best that it can be.
  - Optimality is the tool---not the hypothesis that is being tested!
  - The hypotheses to be tested are the assumptions made about currencies and cost/ benefit functions relating currencies to fitness.
  - Start with simple assumptions and only make your model more elaborate if necessary

Example 1:

Northwest Crows and Whelks

Zach 1979

- Crows drop whelks on rocks to break them open
- Several Observations:
  - 5 Meter Drop Height
  - Re-Drop Until they break
  - Choose to drop only large whelks

Optimality Assumption: Crows maximize energy gain per energy spent handling whelks.

Hypothesis to be tested:

- Crows behave as they do because their energy gain is highly dependent on getting the whelk to break.

- Tests:
  - Drop whelks from different heights
  - Drop different sized whelks

- Results:
  - Large whelks break more easily
  - (Small whelks almost never break)
  - Probability of breakage the same for each drop
  - Increased breakage minimal above 5 m

Example 2:

NW Crows and Littleneck Clams

Richardson and Verbeek 1986

- Crows must find clams in the sand and dig up
- Once they dig them out, they drop them on rocks to break them
- Mussels of 29 mm are abandoned without even trying to open them 50% of the time.
- Mussels >32 mm are always dropped on rocks

- The obvious Hypothesis, extrapolating from Zach:

  Hyp #1: Large clams break more easily

- <u>The Test:</u> Not true!!

- The Revision:

  Hyp #2 Little clams are left behind because larger clams yield more energy

- Measurement of mussel energy content is consistent with Hyp #2

Example 3:

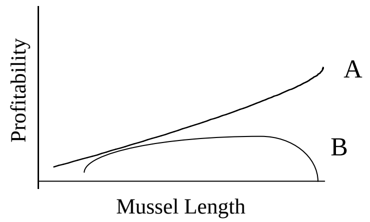
Oystercatchers and Mussels

Meire and Ervynck 1986

- Oystercatchers eat mussels, but break them with their beaks.

- First M & E only looked at the energy content of mussels that birds successfully opened.
  - Large ones took longer but were still more profitable

  Hyp. 1: Oystercatchers should utilize the largest mussels they can find

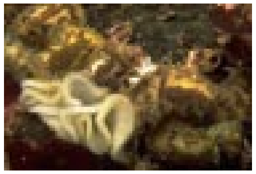


Hypothesis 1 is based on Model A
•OOPS! Reconsidering the data, some large mussels are impossible to open.
•Leads to Model B which yields

Hyp 2 An intermediate size will be optimal

The Model Predictions didn't quite fit the data:

Finally it was discovered that length was confounded with barnacles. Barnacles interfere with opening, and are more likely to be found on some (but not all) big mussels.

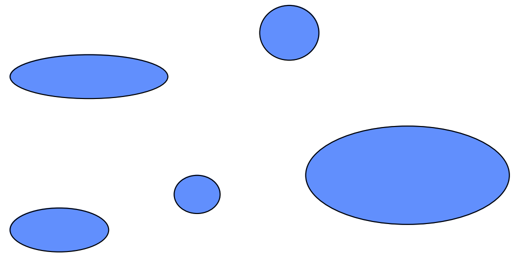


Key Point = Constant Revision of Hypoth.

Moving to a related, but new topic:

Foraging in Patches

•Environments are not always "repeatable" as assumed in MacArthur and Pianka's model
•Food is typically clumped. Examples:
  • Grubs in logs
  • Flowers of particular plant types
  • In Seattle--Lawns for geese and robins
•How a Theoretical Ecologist Might View Patches:



Forager must now search for patches and then decide how long to stay in each patch.

The Patchy Env. Problem

Example: Great Blue Herons and backyard fish ponds

•The Habitat consists of all the fish ponds the GBH can visit
•The Patches are the fish ponds themselves
•GBH seriously reduces fish abundance---diminishing returns over time in each patch

• Decision that must be made: at which point does the GBH decide that patch profitability has been reduced enough that it is time to move on to a new patch.

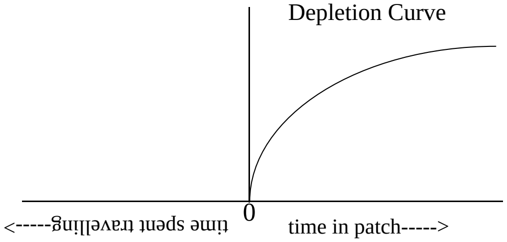
Another classical graphical result

The Marginal Value Theorem

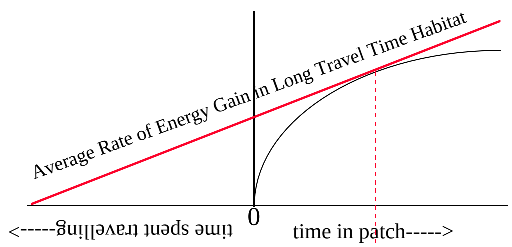
Charnov 1976

<u>Assume:</u>
•Many copies of one type of patch dispersed through the habitat
•All patches have the same "depletion curve"
•Fixed travel time/costs between patches
•Desire to maximize long-term average energy gain

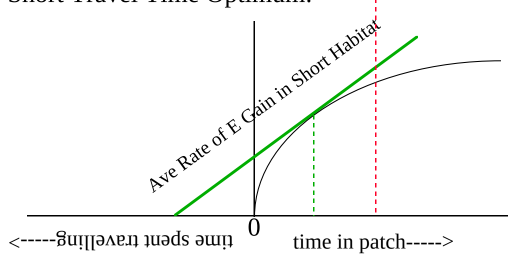
•<u>Bizarre Axis System:</u>



Long Travel Time Optimum:



Short Travel Time Optimum:

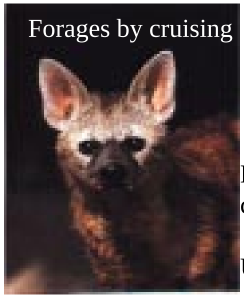


Basic Results of MVT

• Forager should leave patch when its instantaneous rate of energy (food) gain is equal to the average rate of food gain (averaged over the whole habitat)
•Longer average travel time between patches should lead to longer patch residence times
•Could extend to variable patch quality; foragers should stay longer in better patches

• Empirical work on seeing if animals respond to MVT-based cues is very difficult
• Hard to discriminate which cues the forager is really using to make decisions about staying in patches
•Consider observations on the aardwolf, *Proteles cristatus*, foraging on patches of its favorite termite species, *Trinervitermes bettonianus*, in the Serengeti.

Aardwolf seeking termites



Forages by cruising over the grasslands slowly, Starting 3 hours before dark and continuing until dawn.

Don't seem to use olfactory cues to locate termites

Use their ears instead!

(They cancel all foraging for rainstorms---can't hear the termites!)

When they find a colony of termites they root through the dirt with their noses, and lick up the termites

After they've left though, you can run over there and still find plenty of termites milling around, just there for the taking? Why did they leave the patch?

Answer: Soldier Termites filled with terpenoids.

So, do you say that they are leaving the patch because they have depleted the edible termites, or are they leaving because they can't stand the taste?

SO WHAT? The point is that there are many cues that animals may respond to.

<u>Other issues</u>:

•Is it reasonable that animals can monitor "instantaneous rate of food intake" when prey arrive as discrete chunks?

<u>Simpler explanations for patch-staying behavior?</u>

Could be a simple "turning rule" based on how much food has been obtained in the last few minutes.

<u>Search theory</u>: a well developed field of inquiry into these questions

Computer lab this week asks you to optimize intake of a silicon gopher given simple search/ foraging rules.

One arena where MVT ideas/results figure nicely:

Central Place Foraging

<u>Basic Notion</u>: Animals forage outward from a central "home-base" to which they return

Especially germane when animals bring food back:
- Rodents/Squirrels storing food
- Bird foragers bringing food back for offspring

<u>Two Classic Experiments</u>:

•Squirrels feeding on manipulated sunflower-seed patches
- Manipulated distance of different sunflower patches
- Squirrels spent longer feeding at the more distant seed patches, and filled their cheek pouches fuller
- Not a great fit with MVT predictions though (Kramer 1982)

•Starlings trained to get food from a "decreasing profitability mealworm dispenser (Kacelnik)

Maximizing energy gain to self? or energy delivered to chicks?

2 different things!

Multiple Foragers at Once

Simple notion that is often invoked:

The Ideal Free Distribution:

Foragers will disperse themselves amongst patches or across habitats so that their individual gains are maximized

In terms of aggregate behavior this means the animals distribute themselves with respect to both the quality of resources and the number of competitors

Example: Milinski and more stickleback experiments.

IFD assumes that animals are <u>free</u> to move where they want to.

Akin to the <u>ideal</u> gas law

We'll see this again as an assumption in the Cartar paper

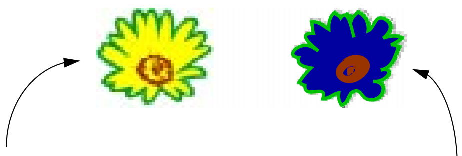
A new topic:

Risk-Sensitive Foraging

Charnov and Stephens

Up until now, the *optimal* in optimal foraging has meant "maximizing the *long-term average* rate of food intake" but consider experiments by Les Real with bumble bees (*Bombus*):

<u>Two Colors of Imitation flower</u>:



all yellows filled with 2 µl of artificial nectar

1/3 of blues have 6 µl
2/3 have 0 µl

So *long term average rate* of food intake would be the same while visiting either flower color.

However, the bees overwhelmingly prefer the yellow flowers.

Further Manipulations by Real:
- Swap Flower colors. So that the blue flowers are the constant ones
  - <u>Result</u>: bees prefer blue then!
- Try a different nectar distribution in "risky" flowers: 2/3 get 0.5 µl
  1/3 get 5 µl

Same result--->Bumble bees don't like to gamble.

Notice: in all of these trials, the *mean* rate of food intake is the same between flower colors, but the *variance* of what the bee gets from any one flower is <u>zero</u> for one of the flower colors (constant 2µl) and <u>positive</u> for the other flower color.

In the jargon of the field we say that these bumble bees are <u>Risk-Averse</u>:
- They will go for the food that gives them the constant reward rate

• The opposite of Risk Averse is called Risk Prone

• Question? Why would any critter in its right mind be risk prone?