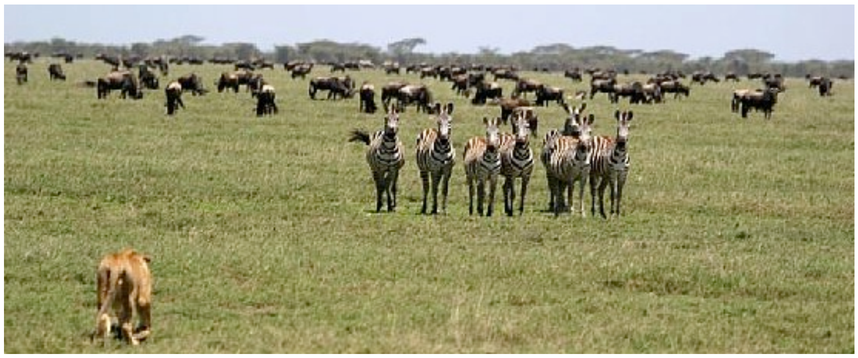
9 Foraging (Notes only)

Consider a predator faced with the option of various types of food: what should it eat?



Three possibilities come to mind. One possibility is that the predator should be opportunistic and grab any prey that it sees. Another possibility is to be more specialized and to actively search for only certain kinds if highly profitable prey. A third option would be to search primarily for the best food, but become less choosy as the predator becomes hungrier. Which strategy would be best?

Our approach is to consider this as an optimization problem. Which strategy will provide the predator with the most energy per unit time? The theoretical justification for using an optimization approach is to say that natural selection will likely favor individuals that use an efficient foraging strategy. We don't know that individuals forage optimally, but we can argue that individuals with the higher foraging efficiency than others will be favored by natural selection. Those individuals that are able to garner the most energy will have higher reproductive success and therefore leave more descendants in future generations. To the extent that the foraging behavior is genetically determined, and ignoring any other constraints, the population should eventually converge on a foraging strategy that maximizes fitness.

In any optimization problem we need a quantity to be optimized. Ultimately we would like to find the strategy that optimizes the fitness or lifetime reproductive success of the organism. But total lifetime fitness is notoriously hard to measure, so fitness proxies are often used instead. Maximizing energy gain is the most common currency used by ecologists. But it is not the only possible choice. In species that suffer substantial predation risk, it may be more important to minimize the search time because that is often a period of vulnerability. Or, if particular nutrients are limiting, a forager may optimize a particular nutrient (e.g. protein or nitrogen) rather than overall energy.

9.1 **Optimal Diet Choice:**

The quantity to be maximized is energy per unit time.
Assume that there are various possible prey items that differ in size or energy content.

The predator must spend time searching for prey. Search time will vary for different prey types depending on their overall abundance (common species are easier to encounter than rare species) or appearance (camouflaged or conspicuous). Once a prey item is found there is additional time required to "handle" the prey. Handling time includes the time it takes to pursue and capture the prey once spotted, or the time it takes to open shells or seeds, etc. The potential **energy gain per unit time** is then

$$\text{Rate of Energy Gain} = \frac{E}{s+h} \qquad 9.1$$

where E is energy content of a particular food item
s is the search time
h is the handling time.

Another quantity to consider is the "**profitability**" of a prey item. The profitability is the expected energy gain *once a potential prey is found*. It includes handling time, but not search time.

$$P = \frac{E}{h} \qquad 9.2$$

For convenience we will label the prey items in order of their profitability. Prey type 1 has the highest profitability; prey type 2 has the second highest, etc. Which should the predator eat?

When the predator encounters a prey of type 1, it should always take it because we have defined it as the most profitable prey. But what about prey type 2?
When it encounters a type 2 prey is must decide whether to take that prey or ignore it and continue searching for a more profitable prey. Our model shows that the predator should take prey 2 only if the profitability of prey 2 is higher than the expected gain from continued searching for prey 1.

$$\frac{E_2}{h_2} > \frac{E_1}{s_1 + h_1} \qquad 9.3$$

For example, Scheel (1993) provides the following estimates for the profitability of various prey items used by lions in the Serengeti. The total handling time for each prey type was divided into several components (the time spent hunting, including failed attempts, as well as the time spent consuming the prey). The profitability of prey ranges from 6.8 kg/hr for wildebeest, to only 2.3 kg/hr for Thomson's Gazelles. Search time was defined as the number of herds encountered per hour.

Table 9.1. Energy, search time and handling time for various prey types used by Serengeti lions. Species are ranked by profitability. Search time varies by season, depending on whether or not the migrating herds are present. (adapted from Scheel, 1993)

				Migrants present:		Migrants not present	
Species	**Kg**	**h**	**P=E/h**	**s**	**E/(h+s)**	**s**	**E/(h+s)**
Wildebeest	85	12.5	6.8	2.6	5.6	250	0.3
Zebra	82	12.3	6.7	4.1	5.0	125	0.6
Warthog	37	6.8	5.5	17.8	1.5	8.6	2.4
Grant's Gazelle	27	8.0	3.4	10	1.5	5.5	2.0
Thomson's Gazelle	3.5	1.5	2.3	5.7	0.5	10.6	0.3

During the rainy season when Wildebeest and Zebra are abundant, what should lions include in their diet? Wildebeest are the most profitable prey of this set, so they will always be chosen if available. What about Zebra? Should the lions hunt a group of zebra or continue searching for wildebeest? The expected profitability from the zebra is 6.7 kg/hr whereas the expected gain from continued searching is only 5.6 kg/hr. It is more efficient for the lions to take the zebra when encountered.

Continuing down the list, should lions include warthogs in their diet or continue searching for more profitable prey? These data show that the expected profitability of a warthog is 5.5 kg/hr, whereas continued searching for a herd of wildebeest would yield 5.6 kg/hr. The lions would maximize their energy gain by skipping the warthog and continuing to search. Gazelles have even lower profitability. Therefore, during the rainy season the lions should specialize on wildebeest and zebra.

Which species should be eaten when migrating herds are absent?

9.2 **This simple model makes some very interesting predictions.**

The first is that a predator foraging optimally should exhibit an "all or none" diet choice strategy. It should either always take a particular prey type when encountered, or always ignore it and continue searching. It doesn't matter what the search time for prey 2 is. Even if prey 2 is extremely abundant and easy to fine, it will pay to eat prey 2 only if its profitability is greater than the energy gain of continued searching for prey 1. Similarly, it doesn't matter what the density of any other low-quality prey is.

A second prediction is that as food becomes less abundant, the optimal predator should add additional items to its diet one by one, in order of their profitability. If the most profitable prey becomes scarce enough that the profitability of prey 2 is higher than the gain from searching for prey 1, then prey type 2 should be added to the diet. Any less profitable prey should continue to be ignored.

Or, stated another way, if foragers are limited by search time, then generalists have higher total rate of energy gain. If prey are abundant so foragers are primarily limited by handling time, then specialists have a higher total rate of energy gain.

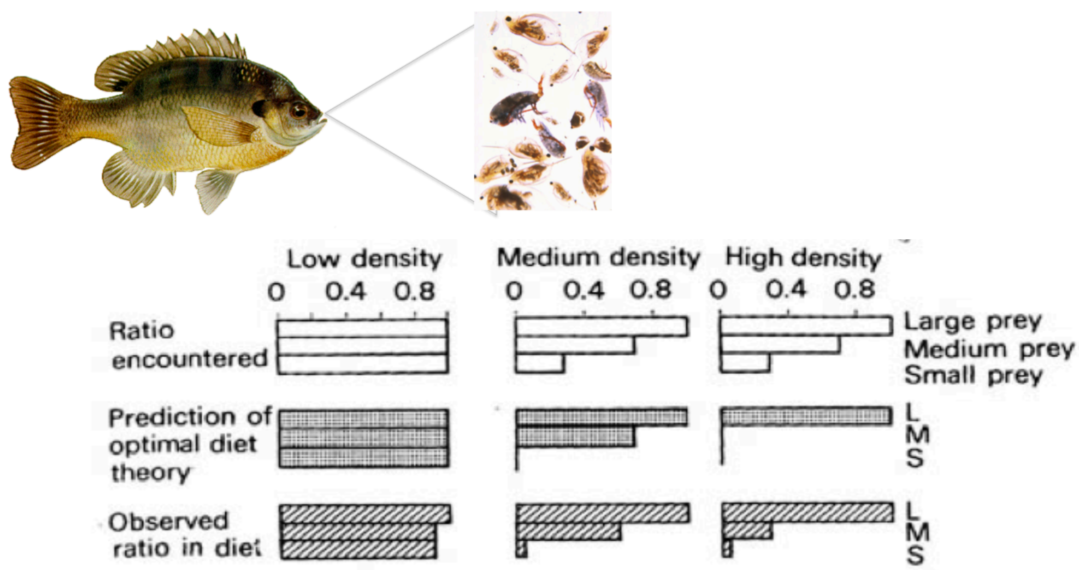
9.3 **Assumptions**

- foragers are maximizing the rate of energy gain
- foragers have complete knowledge of the profitability of each prey item

9.4 **Evidence:**

There have been numerous tests of those results. In general, the qualitative predictions of the theory are well supported. When food becomes more abundant, the number of items included in the diet decreases. However, few if any real foragers use the all or none rule.

For example, Earl Werner studied the diet selection of bluegill sunfish. With low prey density the fish ate prey items in proportion to their availability in the habitat. When prey became abundant, the fish ate primarily large prey items and ignored the small ones. But they didn't ignore them completely.



Why did they continue to sample the less profitable prey? There are lots of possibilities. In general, when data do not match predictions it means that one or more of the assumptions are not met. Therefore some likely possibilities are; 1) perhaps the fish can't recognize the different types of prey. 2) perhaps the fish don't have complete knowledge of the possible prey and therefore continually sample the various food items. 3) perhaps there are constraints other than energy that affect foraging decisions.
All of those lead to additional predictions that could be tested.

9.5 ***Other foraging topics (to be added eventually)***

- *optimal patch use (marginal value theorem)*
- *central place foraging*
- *ideal-free distribution*

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9.6 **Your turn:**

Bernd Heinrich studied the foraging behavior of bumblebees feeding on the nectar from flowers of several plant species. He was able to measure the potential rewards in terms of μg sugar per flower as well as the time bees required to probe the flower for nectar, as shown in the table below. Search time was not measured directly in this experiment. I have set the search time in that table to be inversely proportional to the abundance of each flower type (so abundant flowers have low search time and rare flowers have a high search time).

> Which species should the bees feed on? How many species should be included in the diet if the bees are maximizing their energy gain (sugar per unit time)

Species	Sugar/flower	Handling time	Search time
Impatiens biflora	2.76	0.093	0.13
Chelone glabra	3.27	0.357	1.33
Trifolium pratense	0.05	0.023	1.00
Galeopsis tetrahii	0	n/a	0.80
Aster novae-angliae	0.023	0.009	0.25
Solidago canadensis	0.0024	0.009	0.31

> Heinrich's results are shown below. Inexperienced bees sampled several flower species. But eventually they specialized only on *Impatiens*. Are those results consistent with your predictions?

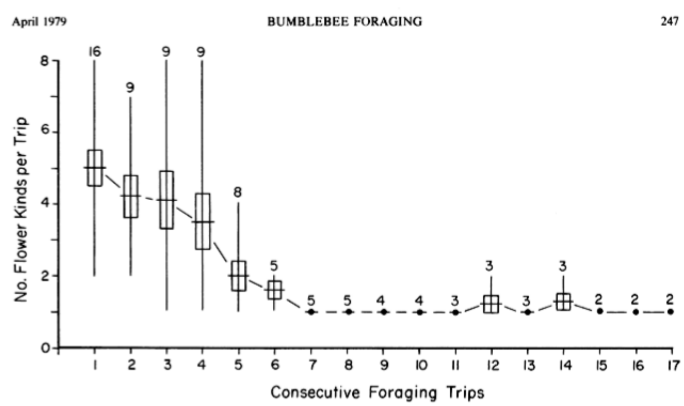

FIG. 1. Number of different kinds of flowers visited as a function of number of consecutive foraging trips starting with the first 1 of the foraging career. "Competition" was held to a minimum (only 1 bee at a time had access to the flowers). All of the trips were completed in 2 days. Numerals indicate sample size. Boxes enclose 1 SE on each side of the mean. Vertical lines indicate range.

9.7 **Answers:**

p 3. When the migrating herds are absent, the prediction would be for lions to eat everything except Thomson's gazelles. The profitability of a Thomson gazelle 2.3, whereas the expected gain for continued searching for a warthog would be 2.4.

p 5. Bees

Species	**Sugar/flw**	**h**	**s**	**Profitability**	**E/(s+h)**
Impatiens biflora	2.76	0.093	0.13	29.7	**12.4**
Chelone glabra	3.27	0.357	1.33	**9.2**	1.9
Trifolium pratense	0.05	0.023	1	2.2	0.0
Galeopsis tetrahii	0	n/a	0.8	0.0	0.0
Aster novae-angliae	0.023	0.009	0.25	2.6	0.1
Solidago canadensis	0.0024	0.009	0.31	0.3	0.0

The bees are predicted to specialize on Impatiens. The expected gain from searching for Impatiens (12.4) is higher than the profitability of the second-best species (9.2).

Notice, however, that the bees still occasionally sampled other species, even after they had learned that Impatiens were the most profitable.