

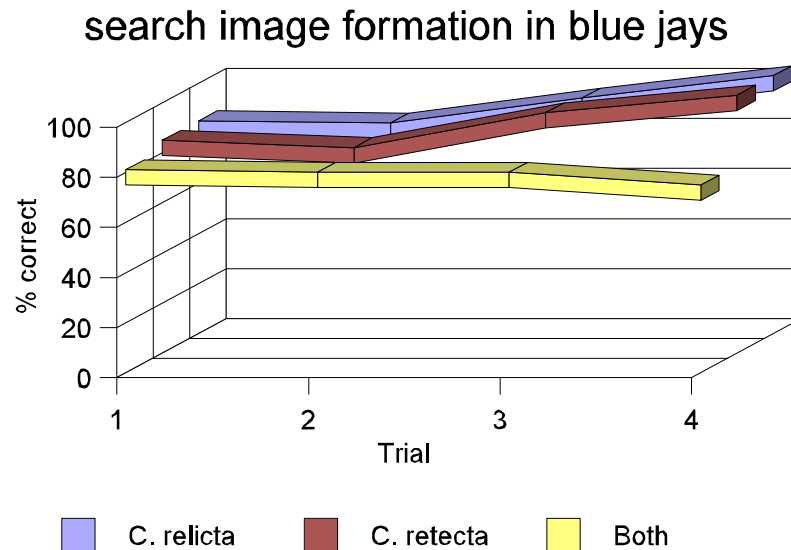
1. In this chapter, we'll use optimality thinking (and a variety of specific models) to explore some of the behavioral adaptations animals use to acquire food. One important take-home message is that optimality models let us develop hypotheses that, if rejected, are very useful in directing our attention to factors not considered in the original model – letting us improve our understanding of the behavior in question.
2. The sequence we'll use follows a typical feeding sequence:
 locating food → deciding what to eat → capturing prey → consuming food
3. When we ask questions about the adaptive nature of specific behaviors, we'll generally use factors relating to the efficiency of food harvest as our performance measure (i.e., our indirect fitness advantage).

CHAPTER 10: ADAPTIVE FEEDING BEHAVIOR

A A wide range of behaviors may be used to help an animal locate suitable food.

1. Many species use **search images** to help them locate favored kinds of prey
 - a. Def = set of (sometimes subtle) visual cues reliably associated with specific prey
 - b. presumed to increase the efficiency with which predators locate specific kinds of prey (especially cryptic ones)
 - c. apocryphal story about origin: term developed by a German ethologist who couldn't find the bottle of water on his table because he was looking for a waterskin – common kind of experience for people!
 - d. e.g. in blue jays:
 - i. jays trained to respond to pictures of moths, then exposed to series of 16 slides – 8 with moths, 8 without
 - ii. in one trial, moth slides all featured same species; in another, two species with different patterns used (in random order)

- iii. in trials with only one species, jays improved ability to correctly identify moth slides over time; in trials with both species, performance actually declined:



- iv. presence of two species prevented formation of search image
2. Social species can share information (directly or indirectly) about the location of food
- a. best known example = honeybees
- i. Note: “worker” bees sterile; benefit is not to own offspring, but to siblings (because of haplodiploidy, may be “more related” to siblings than they would to their own offspring)
 - ii. communicate via “waggle dance”:
 - (a) orientation of straight run relative to gravity gives direction relative to the sun
 - (b) length of straight run, rate of dancing (#circuits/time), frequency of sound gives approximate distance to hive
 - iii. Benefit seems obvious, but worth asking what specific performance

advantage does dancing provide? Three hypotheses have been proposed, tested by Seeley and Visscher

- (a) Dancing scout helps nest mates find food faster than they would otherwise
 - (i) prediction = recruits will find indicated food sites faster than scouts will find new food sites
 - (ii) not met: scouts took ~ 90 minutes to find new food sites; recruits took ~ 2 hours each to find indicated food sites
 - (b) Scouts direct recruits to better food sites than recruits would otherwise find on their own
 - (i) prediction = recruits should bring back more pollen and nectar from indicated sites than scouts bring back from “unguided” trips
 - (ii) met: recruits, once they find an “indicated” site, make several productive foraging trips; scouts often return with nothing
 - (c) Recruitment of colony mates allows lets members of the colony exploit a good site more rapidly before it’s found by competitors
 - (i) prediction = indicated site should show rapid buildup of workers after danced
 - (ii) met: scouts visited experimental sites once every 5-10 minutes; after “danced” the site, built up large numbers of workers over short period of time (even though average time for recruits was 2 hours, enough found the site earlier to give rapid buildup)
- b. Colonies or other aggregations of birds may act as “information centers”:
individuals may follow successful foragers to food sources
- i. several central predictions can be tested:
 - (a) if information is being shared (“purposely” or otherwise), foraging birds should leave roosts at ~ same time, head in ~ same direction
 - (b) when there are “followers” and “leaders”, followers should be

individuals previously unsuccessful at foraging while leaders should be successful

(c) followers should be more successful at finding prey than individuals that don't follow successful foragers

ii. predictions have been tested (with mixed results in several species):

(a) colonial barn swallows exhibit

(i) synchronized departures, common direction

(ii) no evidence of "successful leaders" or "unsuccessful followers"

(b) black-headed gulls showed no evidence of following successful foragers in spite of strong visual evidence of foraging success

(c) ospreys use each other to improve foraging on fish forming large schools that are unpredictably located: following successful foraging by one individual,

(i) others more likely to begin foraging

(ii) likely to head in same direction as successful forager

(iii) spend less time before successfully capturing fish

3. Many species use deceptive signals to attract prey

a. angler fish lures

b. bolas spiders create sticky ball of silk infused with scent identical to specific female moth pheromone – male moth gets stuck on ball and eaten

c. golden orb-weaving spider uses yellow silk to build webs, exploiting preference of tropical stingless bees for yellow flowers

d. garden spiders use uv-reflecting silk to "decorate" webs – apparently to attract insects that uv -reflecting patterns on flowers to locate nectar/pollen sources

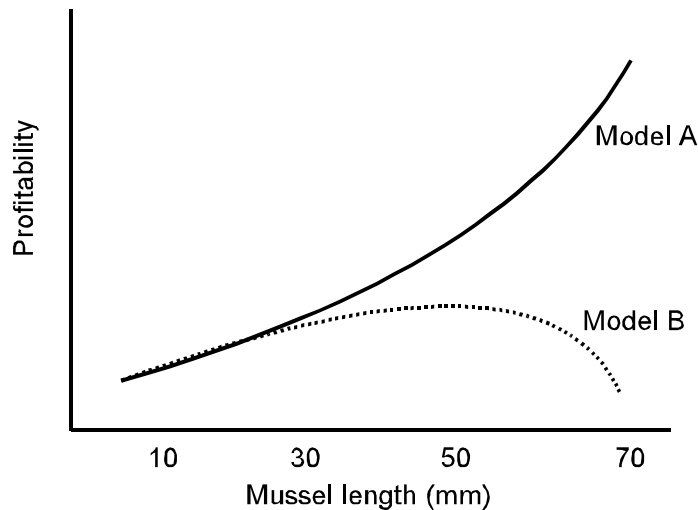
B The choice of what to eat (out of a range of available food types) can be influenced by characteristics of the food, by predation risk, and by the behavior of other individuals in a population

1. Using optimality thinking can help us make sense out of apparent Darwinian puzzles
2. E.g. #1: Howler monkeys appear very inefficient when foraging on leaves, until potential plant toxins (alkaloids and tannins) and nutritional value of leaves taken into account:

Foraging rule	Function
1. The more common a tree species, the less likely monkeys are to select	1. The most common species have the highest alkaloid and/or tannin concentrations
2. Monkeys are highly selective about which individuals of each (rare) species to feed on (e.g., 12 of 149 specimens)	2. Individuals chosen have lowest alkaloid/tannin concentrations
3. Monkeys prefer scarcer, smaller new leaves to larger, more abundant older leaves	3. New leaves have more water, less nonnutritive fiber; among older leaves, selected ones have higher protein levels
4. Monkeys eat only petiole, not leaf blade	4. Petiole is lower in toxins than blade

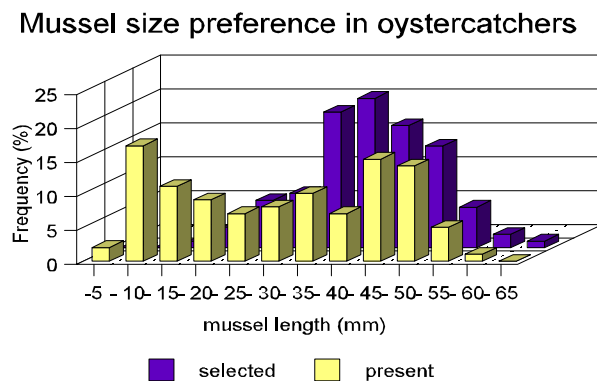
3. Oystercatchers select a small range of available mussels: can use optimality models and tests to figure out why, based on profitability of prey:
 - a. large mussels return more calories than do small mussels, even though they take longer to open – so optimal strategy should be to feed preferentially on larger mussels (see “model A” on graph below)
 - b. but oystercatchers feed preferentially on medium-sized mussels, mostly avoiding larger ones – why? what’s missing from the model?
 - c. hypothesis #1: large mussels are so hard to open that their profitability (calories gained - calories spent) is less than for medium-sized mussels

- i. model revised to take into account individuals that are so big that they must be abandoned before opened:



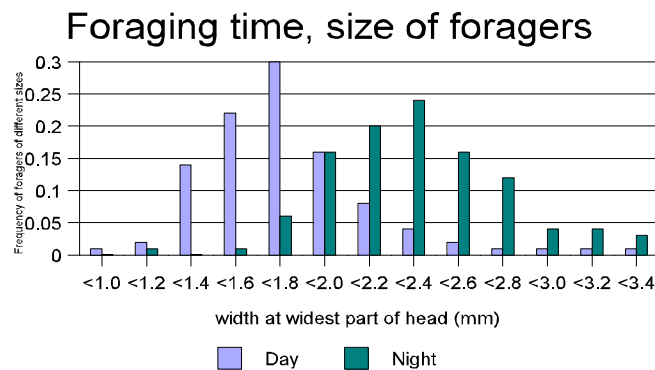
- ii. predicts that oystercatchers should feed preferentially on mussels ~ 50 mm
- iii. actually prefer mussels in the 30-45 mm range – something still missing
- d. hypothesis #2: many large mussels are not even worth attacking because they're covered with barnacles, making them impossible to open (i.e., as far as the oystercatchers are concerned, these aren't even included in the range of prey available)

- i. oystercatchers “never touch” barnacle-covered mussels
- ii. the larger the mussel, the more likely it is to be covered with mussels
- iii. mathematical model



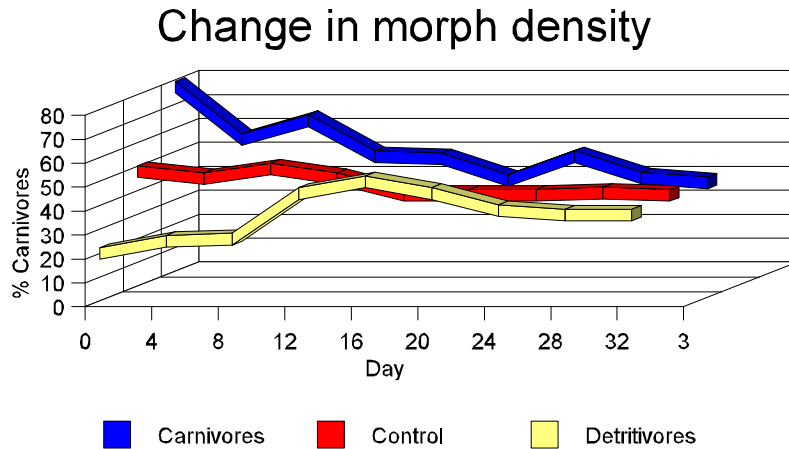
incorporating all 3 factors (time, cost of trying but failing to open large mussels, actual range of non-barnacle covered mussels) predicts 35-40 mm prey as optimal size – exactly what they do (note that this is unusual!)

4. Foraging in leaf-cutter ants is affected, in part, by cost of predation risk
 - a. efficiency of foraging is a function of head size: individuals in 2.0 - 2.6 mm range most efficient
 - b. if maximizing food return to colony were only factor in foraging “decisions”, only these ants would forage, and would forage day and night
 - c. but find that :
 - i. relatively few ants forage during the day, and the ones that do are smaller than optimum;
 - ii. optimally-sized ants forage almost only at night – why?



- d. ants are attacked by parasitic fly:
 - i. lays eggs in heads of ants
 - ii. is diurnal
 - iii. doesn't lay eggs in small workers (presumably because heads are too small to provision larvae)
- e. so, pattern makes sense:
 - i. nocturnal foragers of all sizes are safe from flies
 - ii. small foragers are safe at night

- iii. so colony reduces short-term gain in return for longer total foraging life of most efficient foragers
5. New Mexico spadefoot toad tadpoles make foraging “decisions” based, in part, on what other individuals in the population are doing
- a. when costs/benefits of a particular behavior are affected by behavior of others, the type of optimality model used = **game theory** – this will be a qualitative example
 - b. larvae can take on one of two morphs (similar to salamanders):
 - i. rapidly-developing carnivore feeding on fairy shrimp
 - ii. slower-developing detritivore
 - c. rapidly-developing carnivore metamorphoses earliest, which should be advantageous in temporary ponds – so why don’t all larvae do this?
 - d. important clue: this “developmental switch” is facultative and reversible: as density of fairy shrimp decreases, carnivores can “revert” to detritivores
 - e. Hypothesis = feeding mode depends on prey availability – which, in turn, is a function (in part) of the relative proportion of the two morphs in the populations.
 - i. prediction = each pond should have ~ equilibrial number of each morph (exact number of each will depend on prey density and possibly other conditions)
 - ii. Pfennig tested by partitioning 5 experimental ponds into experimental and control compartments, then altered the density of carnivores in one compartment
 - iii. found that , in all 5 ponds, proportion of carnivores in experimental compartments reverted relatively quickly to that of control compartment. (e.g. from one pond)



- C Capturing a desired prey item may require special handling, “teamwork”, and/or “decisions” about the timing of foraging activities.
1. Noxious prey types – e.g., insects with chemical defenses, may require “special handling” strategies:
 - a. e.g., tenebrionid beetles spray noxious chemicals
 - i. grasshopper mice jam abdomens into ground, bite off heads
 - ii. skunks roll beetle around the ground with forepaws until chemicals depleted
 2. For some prey types, social foraging may be beneficial:
 - a. schooling fish can separate to confuse/confound predators
 - i. gulls often forage for schooling fish in flocks – does this help counter fish behavior?
 - ii. gulls allowed to forage in groups on schooling fish had higher success rates per individual than did gulls foraging alone – because fish trying to escape from one gull often wound up swimming toward another
 - b. social carnivores can use cooperative hunting to take larger prey than individuals would be able to manage on their own
 - i. can use optimality models to understand group size – obvious prediction

- is that chosen group size gives optimal return in terms of food intake
- ii. when food intake alone measured, prediction not met – in several studies of African lions, individuals in groups of 2 or more consumed less food than did individuals hunting alone
 - iii. however, that model doesn't take into account the costs of hunting – just the benefit in terms of food acquired
 - iv. Scott and Martha Creel revised model for African hunting dogs to include the costs of hunting
 - (a) measured cost in terms of distance traveled in high-speed chases
 - (b) new model yielded lower optimum group size than did model based just on energy return (benefit)
 - (c) but new model still predicts larger group sizes than actually seen – so, although second model more realistic than first, more factors still need to be included
3. When individuals are foraging away from offspring or shelter, must make decisions about the timing of activities – can use optimality to explore
- a. one e.g. = how long to spend gathering food before returning to nest:
 - i. as number of food items collected increases, additional benefit of each new food item declines because
 - (a) efficiency of handling decreases
 - (b) density of prey decreases
 - ii. therefore, “law of diminishing returns” predicts that each animal should have “optimal quitting time” = point at which adding one more prey item costs more than it's worth in terms of extra food benefit
 - b. Optimal quitting time will depend on several factors, including which specific factor foraging individual is “trying” to optimize: e.g.
 - i. **rate of energy extraction** = calories gained per unit foraging time
 - (a) **Yield = NV/T** where

- (b) N = number of prey
V = useful energy per item
T = total foraging and delivery time
 - ii **family gain** = energy available for growth of nestlings (similar, but not identical, to above)
 - (a) this will be yield (from above) less:
 - (b) Energy spent by foraging parent, maintenance energy for nestlings:
 - (c) family gain = $NV/T - E_p - E_c$
 - c. Kacelnik experimented with starlings to see which of the two models best explained quitting time when foraging on mealworms at different distances from nest
 - i. when experiment included decline in mealworm availability with foraging time (mimicking depletion of food patch), family gain model did better at predicting results than individual yield model
 - ii. but, when provided mealworms ad lib (no decline in availability with foraging time), got anomalous results:
 - (a) both models predict that, if prey abundance doesn't decline, the number of prey gathered on each trip should be the maximum that can be carried (5)
 - (b) found, though, that starlings stopped at 2-3
 - (c) decided that some cost had been overlooked in the model – cost of transporting additional prey
 - iii. found that, the larger the number of mealworms, the longer it took individuals to return to nest – a very surprising result given that mealworms weigh ~ 1% of adult starling's weight (so using optimality revealed something that no one would have expected initially!)
- D Consuming food may require additional preparation and/or decisions about when/where to consume captured prey items.

1. some prey items require additional handling before they can be consumed:
 - a. loggerhead shrikes impale prey on thorns (or barbed wire!) – in addition to “storing” food, this allows noxious chemicals to degrade
 - b. northwestern crows drop whelks to crack them open – but needs to decide which whelk to select, how high to fly, and how many times to drop it before giving up
 - i. Zach observed pattern of crow feeding:
 - (a) only dropped large whelks
 - (b) only flew ~ 5 meters to drop selection
 - (c) kept dropping whelk until it dropped – even if many attempts required
 - ii. hypothesized that this was optimal pattern in terms of whelk flesh available for consumption per unit time spent foraging (note how simplistic this is relative to others we’ve discussed)
 - iii. tested predictions using experimental apparatus that let him drop whelks from different heights:
 - (a) large whelks should be more likely to shatter after being dropped 5 m than small whelks – met
 - (b) drops of less than 5 m should greatly reduce shattering rate, but drops of more than 5 m shouldn’t increase it much – met
 - (c) the probability that a whelk will shatter is independent of the number of times it’s already been dropped (so crow dropping a whelk after any number of drops has no better chance that the next one it catches will shatter – and the next one still has to be found and captured) – met
 - iv. also calculated caloric gain and cost of opening whelks of various sizes – found that medium - and small-sized whelks (which require more drops) actually require more energy to open than they return in food– supporting, in this case, a fairly simple optimality model
2. Another important decision is where to eat captured food – where it’s captured

(minimizing energy) or , e.g., in a sheltered location (minimizing predation risk)

- a. optimal strategy should be to
 - i. select sheltered location if predation risk is high or
 - ii. if cost of travel to sheltered location is low
- b. Lima tested prediction that moving to sheltered location should increase as cost of travel to shelter decreases
 - i. provided feeding trays at different distances from dense cover
 - ii. if birds simply optimized energy intake, should stay at one tray and continue to feed (minimizing cost of travel), regardless of distance to shelter
 - iii. birds often took food to shelter; tendency to do so increased the closer they were to shelter
- c. Then tested prediction that moving to sheltered location should increase as (perceived) predation risk went up
 - i. using same setup, exposed birds to model hawk moving overhead while birds were at feeders
 - ii. as predicted, birds carried more food to cover over all distances after exposure to predator

E On your own, read about “when to eat dirt”!