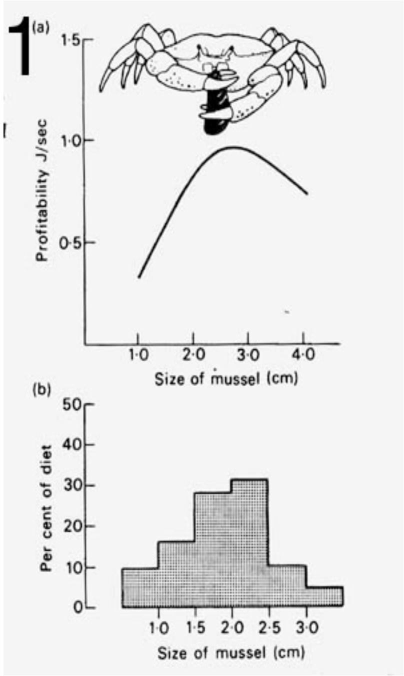
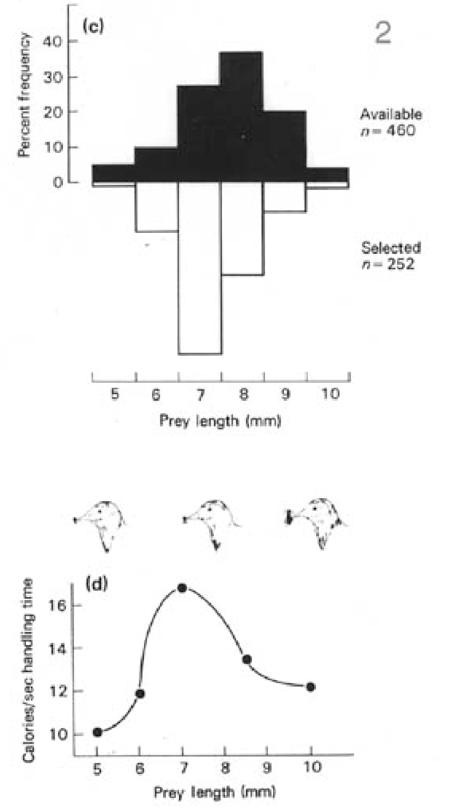
Bio 45 –Lect. II –2/3 - **Optimal Foraging Models --Diet Choice Models**

Basic Process:

Remember that our goal is to make a model of how an animal is expected to forage under certain conditions if it is foraging optimally. We will test our model by way of predictions it makes about foraging behavior. You will read a fairly complex presentation of a diet choice model in the oystercatcher paper next week. Here we will step back and look at some of the basics of doing diet choice models.



Example 1. What size mussels should crabs include in their diet? We give a group of crabs mussels of different sizes and see how long it takes them to open and eat each mussel. We also measure the calories contained in each mussel of each size. We can then use these data to calculate the profitability of different sized mussels (see top graph in figure1). **Profitability** is the total energy contained in the prey divided by the time it takes to get that energy (open and eat). Here we are using time as an index of energy spent. Ideally we would calculate the energy used to consume food -- profitability = energy in mussel minus energy it took to get it. The **profitability curve** in figure 1 shows that as mussel size increases so does the relative profitability -- up to a point. Then the return of energy decreases with size because of the increased cost of getting that energy. The peak for the curve tells us **the most profitable prey size to take**. We then go out an measure what size mussels crabs in nature eat (lower graph in Figure 1).The majority of mussels eaten were in the 1.5 to 2.5 cm size range which is close to the 3.0 size range predicted by our model. Can we conclude that the crabs fit the prediction of our model? No. There is another hypothesis we ned to consider that could equally well explain the pattern of the data we collected. Suppose crabs eat any mussel they find (random sampling). This would be our **null hypothesis** (the crabs are not selecting certain size classes). In order to test between our first prediction and the null prediction (no choice), we have to either 1) give them a random collection of sizes to choose from and show that they eat a non-random sample from that collection, or 2) show that the distribution of mussel sizes in nature differs from the distribution of mussels sizes eaten. Thus our study so far is weak -- no null hypothesis tested.



2.2.2 Optimal breadth of diet depends on prey availability

🡐 **Example 2.** Figure 2 shows the results of a study on redshanks (a large sandpiper) feeding on worms in a mud flat. Here you can see the profitability curve (below) and the size distribution the birds took (open bars). They also sampled the same areas to see what sizes of worms were actually there (black bars). It is easy to see that the birds took a biased sample of available sizes and one that agrees fairly well with the predicted optimal diet.

These studies show that the fit to the predictions, although close, are not exact. How do we explain why they are not? Did we go wrong with the model or some of the assumptions we made? Did we measure or calculate things wrong? Did we miss other constraints on diet choice that explain what the animals were doing? How do we decide if we are satisfied that we learned something about how these animals actually forage?

Over 🡒

The Next Step:

So far our procedures do not tell us what a forager should do as the density of the available prey changes. **Optimal diet models** predict that as the density of the most profitable prey type increases, foragers should switch **exclusively** to it. Thus diet breadth (number of kinds of prey taken) should vary with the density of the most profitable prey type. This seems to make sense. But, it means passing up any less profitable prey that falls into your lap! The model also predicts that adding lots and lots of the less profitable ones should not cause a switch back to a broader diet. Should a predator really pass up prey that it already has to look for another it hasn't got yet?? These predictions are somewhat counter-intuitive. It is an important prediction of the model. Here is a way to think about it.

Suppose our predator lives in a world with only two sizes of mussels -- large and small. Suppose forager "**big"** specializes on large mussels and forager "**both"** eats large and small sizes. Large mussels have twice the profitability of small ones. Our foragers bump into mussels at random and they bump into one mussel at a time and cannot see what size the next mussel will be. Under what conditions will forager **big** make a greater profit than forager **both**?

If there are only large mussels around (and enough of them) then both **big** and **both** do equally well -- right? If there are only small ones around then **big** starves to death and **both** does fine (assuming there are enough small ones to satisfy its needs). Now let's start adding large mussels to a population of small ones. At what point (conceptually) does **big** get back in the game? When it encounters large ones often enough to stay alive. But at that point (number of large ones has increased) does **big** make a greater profit than **both**? Let's say **big** bumps into a small mussel and passes it up, **both** bumps into the small mussel and eats it. **Both** is ahead in making a profit. Now **big** bumps into a large one and eats it while **both** hits a small one and eats it. They are even at this point. Suppose that large mussels are so rare still that **both** finds and eats three small ones before **big** finds and eats another large one -- **both** is still ahead (1.5 vs. 1 in the same amount of time).

As long as there are not many large mussels around, **both** will, on average, do better. As we keep increasing the absolute number of large mussels what will happen? It is easier to see if we make 50% of the mussels large and distributed them randomly so that each forager encounters a large one then a small one, then a large one, etc. Note that the order of encounter (or **chance of encounter**) is determined by the proportion of each mussel size in the population. How long it takes to encounter (or **rate of encounter**) the next mussel depends on the overall density of mussels (e.g., # per square meter). The more mussels there are, the shorter the time between encountering any two mussels. Remember that **both** always stops to eat each mussel it encounters -- that takes time. **Big** skips small ones and spends the time it would take to eat them looking for the next mussel. There has to be a density of mussels at which **big** not only survives, but does better than **both** because it can find a large mussel in less than the time it takes **both** to eat a small one. Thus the model's prediction: increase the density of the more profitable prey and there is a point at which the predator does best by taking only that prey (**big** does better than **both**). Thus if **big** and **both** are two tactics that each forager can use, the model says that 1) the best tactic to use (take all or limit your diet) depends on the density of the most profitable prey and 2) that once that density is reached you should use only that tactic.

Below are the results of two experiments that tested this model. In each case the proportions and densities of prey types were varied and the expected proportion in the diet was calculated from the model. You should be able to figure out what the null hypothesis predicts. In both cases, at higher densities there was a diet shift toward the more profitable type. The shift was, however, not all or none. Since these early tests much debate and research has gone on over 1) whether or not the models worked, 2) why the animals did not behave as expected, and 3) can we make models that work better. What do you think? What else could explain the difference between the expected and observed results?