Notes on Optimality Theory

Ethology & Behavioral Ecology

***Summary**: These notes explain the procedures and assumptions behind a valuable technique using in studying adaptation called optimality theory. Pay particular attention to the critiques of optimality theory.*

I. OPTIMALITY:

A. Definition and Uses

1. We will see many different examples of optimality models over the remainder of the course. All share one common attribute:

OPTIMALITY MODELS PREDICT THE <u>EXTENT</u> OR THE EXACT NATURE OF A SPECIFIC BEHAVIOR UNDER <u>DEFINED</u> CIRCUMSTANCES.

They do so by looking at the costs and benefits of performing a behavior (for example, selecting food items) in different ways (should one select large or small items) and then finding the particular version of the behavior (for example, selection of a particular size of a certain type of food) that maximizes the net gain in fitness for the animal.

a. For instance, optimality theory has been successfully applied to explain why crows dropping mussels (the mollusk) onto rocks from a certain height as compared to other heights.

1. The question was not whether or not the crows should opened the mussels using dropping versus some alternative behavior such as prying open with the beak or by using an oyster knife!

2. Instead, optimality was used to predict exactly the best height from which the mussels should be dropped -- *i.e.*, the best way to perform the "dropping" behavior given the environmental constraints the crows faced (for instance, the thickness of the mussel's shells).

b. Thus, and this cannot be emphasized too much; optimality models do not look at distinctly different alternative behaviors that may be used in some situation. Nor does optimality modeling examine how different behaviors interact with each other and affect fitness. Investigations of **<u>alternative behavioral strategies</u>** are pursued using a different type of modeling called **<u>GAME THEORY</u>**.

B. Both optimality and game theory involves **MODELING** -- an attempt to understand a complex situation by simplifying it and including only what we feel are the most relevant variables and interactions.

1. In any model, <u>what we gain in clarity comes to some degree at the loss of accuracy since we ignore certain variables</u>.

2. Also, keep in mind that just because there is correspondence between the predictions of our model and the real thing, that this <u>correspondence only suggests that the model is valid</u> . We should always maintain a healthy skepticism of models, although they when tested carefully and refined over time. Like any hypothesis, there is more reason to feel that we may actually understand what is going on the more support a model gains, but we must always remain skeptical.

! Optimality theory can be used to make predictions about the evolutionary causes of any trait, behavioral or morphological. We will generally ignore the latter and will in fact only speak about optimality in behaviors. However, keep in mind that optimality is a powerful concept in biology outside of the study of behavior. For example, it is very commonly used in morphological and physiological studies when competing factors affect the design of some structure (such as wing) or process (such as metabolism).

C. Optimality theory **<u>rests on the assumption that the trait we are examining is an adaptation that represents the best compromise between a number of factors</u>**.

1. As with any adaptation, <u>we assume this compromise maximizes the long-term fitness of its possessor</u>.

2. Of all of the factors that may be involved in shaping a behavior:

a. Which factors are likely to matter?

b. To what extend do they matter relative to each other?

3. Once these variables and relationships have been postulated, they represent a working hypothesis of an optimal condition. This hypothesis must then be rigorously tested.

a. The usefulness of the optimality model is that it can be used to generate a series of specific testable hypotheses as to the causes of a particular behavior.

b. If there is a difference between prediction and result, then the model or suppositions must be re-examined.

c. Keep in mind that **<u>one of the most important pre-suppositions is that the animal in fact does behave optimally with respect to the determinants and traits in question.</u>** We will see at the end of these notes that there are a number of reasons to believe that <u>although animals may approach optimal behavior, they may not always get there</u>.

D. OPTIMALITY is generally **<u>operationally</u> <u>defined as the process whereby the DIFFERENCE between benefits (b) and costs (c) for a particular behavior are maximized.</u>**

1. Notice that it is **<u>NOT</u>** defined as **<u>the point where</u>**:

a. Benefits are greatest

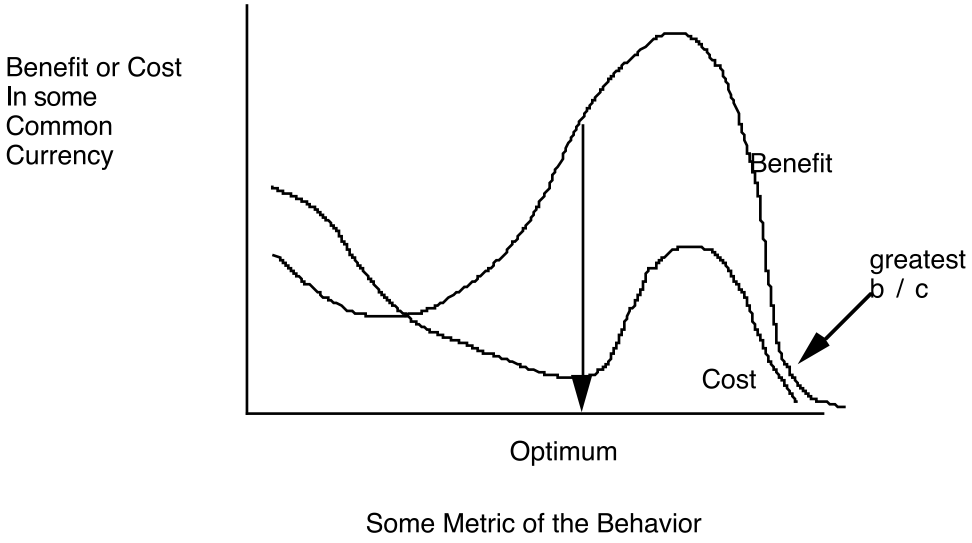
b. Costs are the least
c. The ratio of benefit to cost (b/c) is greatest.

Any or all of these points may in fact correspond to the optimum, BUT THEY DO NOT NECESSARILY NEED TO!

2. One of the easiest ways to identify an optimum is graphically. The graphs typically are constructed with:

a. The benefit or cost on the y-axis and
b. Some measure of the behavior on the x-axis (there are other ways to do it, however):

Optimization #1



! In many accounts, including places in your text, optimality is often defined in terms of the greatest b/c. The problem with this approach is apparent in the above diagram: very small benefits divided by very small costs can yield very large b/c ratios but in fact they result in little real gain to the organism. Thus the crucial payoff to the organism is the TOTAL NET (REALIZED) GAIN. This may be expressed simply as a gain (for instance in calories) or there are other times when it is expressed as a NET RATE OF GAIN -- i.e., NET GAIN PER UNIT TIME.

$G = \{(B-C)/time\}$

We will see examples of different optimality models that maximize gain and rate of gain.

E. Construction of an optimality model -- general principles and an example. Let's flesh out what we have just mentioned above.

1. Principles:

a. The behavior must be clearly defined. We have emphasized this throughout the course. A good model cannot be constructed if we are not even sure about the limits of the behavior under consideration. Moreover, since we are looking at the best way to perform a particular character, a central feature of the definition of the behavior will be **some sort of metric that describes the range of performing the behavior**. We often refer to the behavior whose optimum we wish to discover as the **DECISION VARIABLE**.

Image a male insect or frog calling to find a mate. What feature of the call is the behavior of interest to the optimality modeler? The loudness? Call repetition rate? Total time of calling? Frequency modulation? Number of harmonic notes? Any of these or some combination are suitable for investigation using optimality modeling. Moreover, notice that all can be easily measured -- *e.g.*, call loudness in decibels at some particular location near the calling individual.

b. A common currency must be identified that measures the effects of different values of the decision variable on the costs and benefits of the behavior. This currency must somehow relate to fitness.

i. This can often be one of the most difficult aspects of constructing an optimality model -- some things are easily quantifiable in one measurement system but not in another. We will see an example of this shortly.

ii. Examples of things that are used as metrics of B and C in optimality include:

a. **DIRECT FITNESS** measures such as numbers of grandchildren, children or measures of **INCLUSIVE FITNESS**. This is obviously the most direct currency but it is also often the hardest to measure since it involves looking at the lifetime consequences of single events.

b. **Survival effects** -- measures of the likely change in life span produced by some behavior. Generally an easier currency to get estimates of than inclusive fitness; however, its effects will be different at different times in an animal's life -- extension of life after the end of a reproductive period may, for instance, raise, not affect inclusive fitness at all or perhaps even lower it.

c. **Time** -- presumably any investment in time in one thing means that it cannot be in something else that is also important; therefore it is a measure of cost. Likewise, benefits can also come down to time saved by making one choice or doing one thing as compared to another. We will see an example of time in optimality models next week when we look at mating behavior in that most fascinating of insects, the dung fly. This is a popular currency because it is very easily measured.

d. **Energy or specific material resources**: obviously, the more energy an animal has available to it, then in principle at least the more it has to channel into actions that increase its inclusive fitness. Likewise, the same is true of certain crucial resources such as a territory or particular dietary items such as flower patches for hummingbirds. It also is very easy to measure.

Using our previous example, suppose we are modeling loudness of a frog or insect's call. Costs could be measured in terms of predation risk that could be translated into shortened life and fewer offspring and benefits could be translated into greater numbers of mates. This is obviously related to number of offspring. Alternately, a more derived model might look at loudness cost in terms of energy required to produce a call and benefits in terms of energy saved searching for a mate. But note in both cases that it is crucial to identify currencies that can both be related to costs and benefits. If not, when comparing benefits and costs of behaviors we really will be comparing "apples and oranges".

c. Descriptions of how the costs and benefits vary with the way the behavior is performed must be obtained. This requires identification of the all factors that are believed to be relevant to determination of costs or benefit need to be identified. These factors will generally come into play each time the behavior is produced and their individual values and relative weights must be determined or estimated by the investigator. Obviously, the better the values and inter-relationships are known, the more meaningful[i] the predictions made by the model.

1. For example, assume that there are several components believed to affect the cost C of a behavior. We will call these factors, F_1, F_2 .etc. Moreover, assume that the cost of each of these factors itself varies as some function ***f*** of the way the behavior of interest (example -- the height at which to drop a shell). The approximate idea is that cost is being mostly determined by some function like this:

1. $C = f(F_1, F_2, F_3, .. F_N)$

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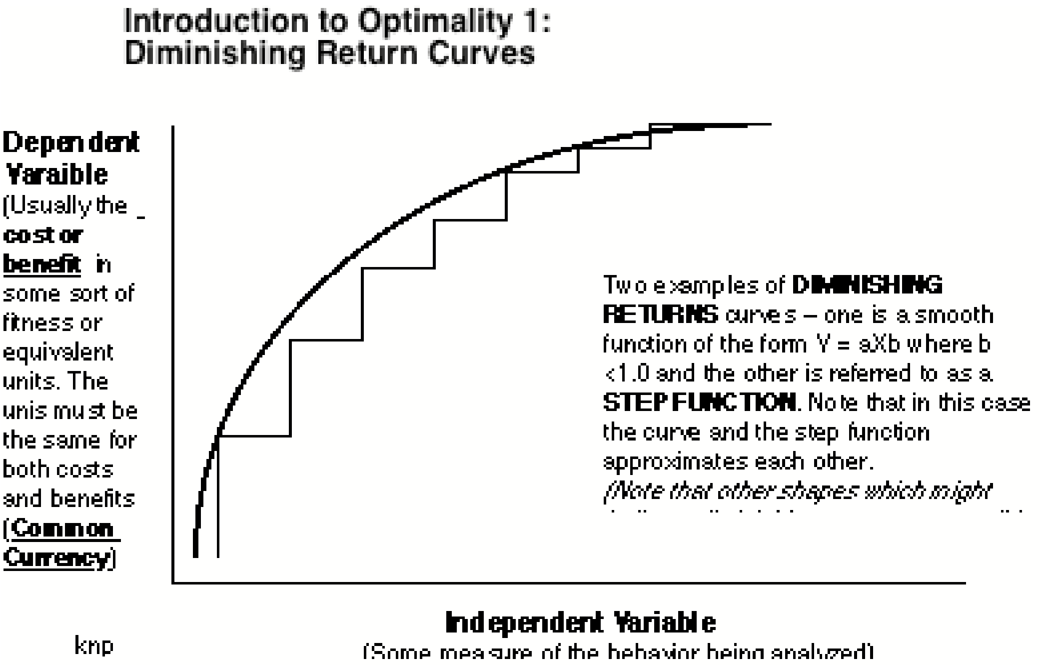
[i] Meaningful here refers to the amounts of confidence we will have that agreement between our model's predictions and our experimental observations is not simply fortuitous.

The resulting function for C can of course be graphed. Sometimes the result is linear but often it is in the shape of what is referred to as a **diminishing returns curve**. One is shown below.



Incidentally, while the curves are often drawn as smooth lines, in fact, the actual predictions are often stepwise and the smooth line is simply an abstraction of the real situation. This is shown in the graph above.

Benefit curves can of course be written with a function similar to the one just presented for costs:

2. $B = \boldsymbol{g}(V_1, V_2, \ldots\ V_N)$

where the function is now represented as ***g*** and the variables that determine benefit by Vs.

? Do you think that both costs and benefits can be represented with diminishing returns curves or are these sorts of curves only appropriate for one of these factors?

d. Careful measurement of the B and C functions can in some cases be achieved directly but in others is achieved by measurements of each variable making up the B and C functions and by careful determination of how they interact.

G. Finally, we need to perform an adequate test of the predictions generated by the optimality model. This is not as easy as it might sound.

i. Recall that most things in evolution are not totally cut and dry -- slight differences may be significant on the average but generally any one given event in an animal's life some slight difference does not affect and organism's fitness.

ii. Animals will not be prefect in their behaviors. One thing assumed in optimality models is that animals have perfect information about the situation that they face and then they act totally rationally according to the principles of optimality.

a. in fact, animals will not always have perfect information -- the crow will not always know the thickness of a shell by its weight, etc. Imperfect information will produce imperfect behavior even if the correct rules for determining the behavior are being followed.

b. Likewise, there may be competing demands on the performing animal that the model does not take into account because they only crop up rarely and have nothing directly to do with the behavior of interest. One of these competing factors may will be the presence of the scientist-observer. This is one reason why we often do work on animals with less sophisticated sensory systems than are possessed by most higher vertebrates -- insects for instance often are relatively oblivious to human observers (but not always -- ask me about my experience observing white-faced hornets at my farm).

THE RESULT OF THESE AND OTHER EFFECTS ARE THAT WE DO NOT EXPECT ANIMALS TO ACT AS AUTOMATONS THAT GENERATE THE BEHAVIOR EXACTLY IN EACH APPROPRIATE SITUATION. THUS IT WILL TAKE A LARGE NUMBER OF DUPLICATIONS OF THE EXPERIMENT TO TEST THESE MODELS. IT IS NOT UNCOMMON FOR BEHAVIORAL EXPERIMENTS TO INVOLVE SEVERAL HUNDRED OBSERVATIONS FOR A RELIABLE TEST.

? Suggest some additional reasons why behavioral studies of animals generally do not produce as cut and dry results as some biochemical system would.

F. An example:

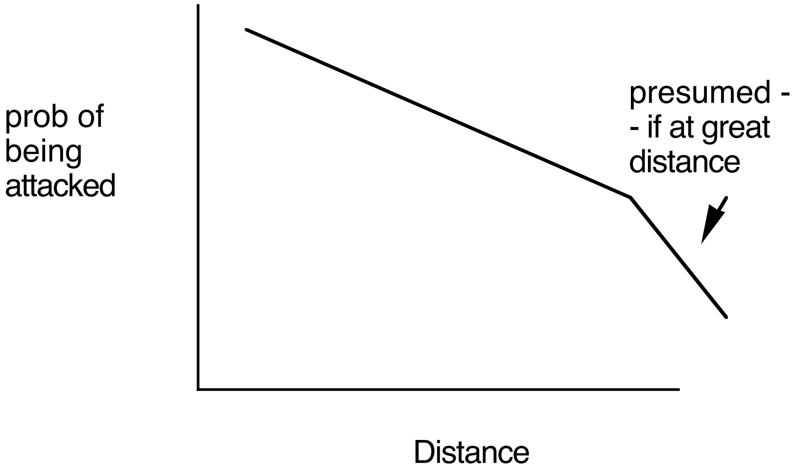
1. **Mobbing behavior** is observed in a variety of different mammals and birds, especially the latter. It consists of sham or even real attacks by several individuals on a potential predator. It is most commonly displayed when the weak (usually young or injured group members) are being protected.

2. **Is mobbing effective**? To answer this we look at Kruuk (1964, Behav. Suppl, v11).

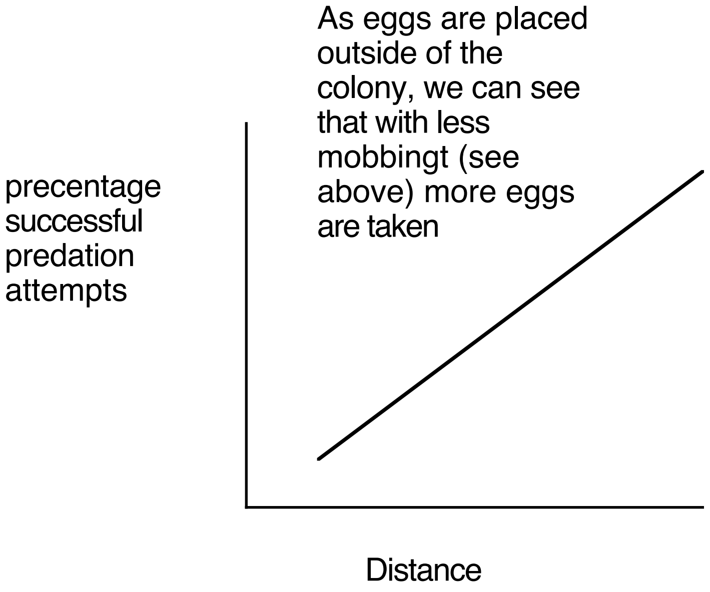
a. He placed <u>**hens eggs inside of black-headed gull nesting colonies**</u> and then **looked to see how successful crows were at taking them and also on where the crows were mobbed the most**.

b. His results (re-drawn):

i) the chance that a crow will be attacked as a function of its distance from the center of the colony:



ii) The chance that a hen's egg will be successfully taken:

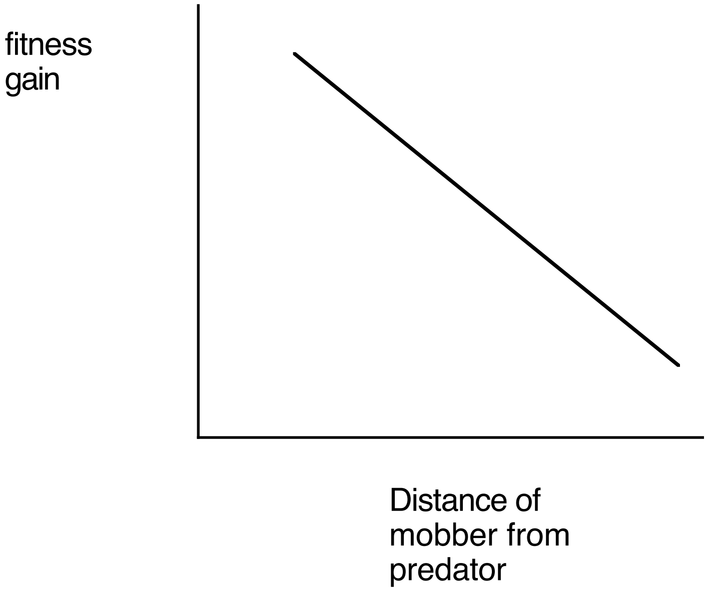


This study clearly shows that mobbing works -- eggs that are outside of the colony where mobbing is less likely to occur (graph 1) are more likely to be taken. Thus, mobbing interferes with the crows.

c. Now the question the optimality theorist would ask -- What is the best way to mob?

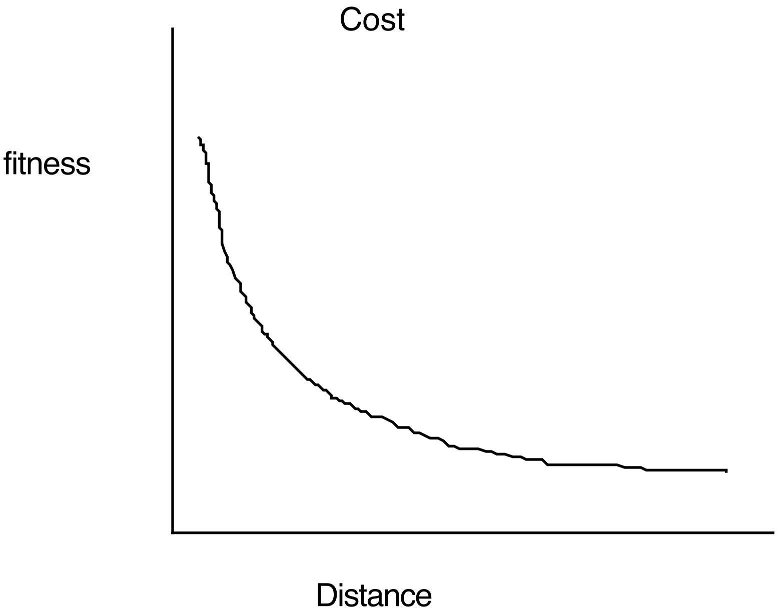
i. Benefits -- anything that decreases the likelihood of predation nest benefits an individual's inclusive (primarily its direct) fitness. How does this look as a function of distance. One very simple relationship that would seem likely is that the closer the mobber comes, the greater the chance or avoiding predation and therefore the greater the fitness gains:

BENEFIT

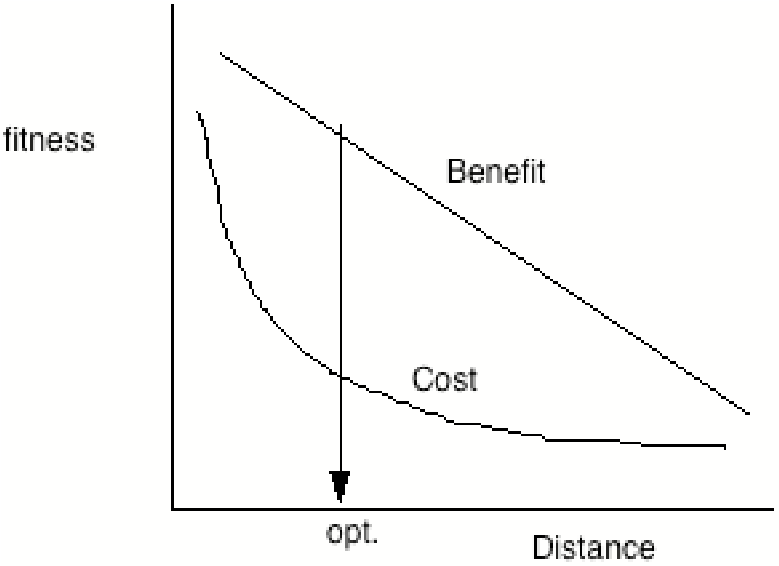


? Will risk be the same at all times in a defender's life? Explain.

The **COST** likewise would seem to be related to distance. If the predator is a formidable opponent, the closer one gets, the greater the risk to oneself. We might envision a graph of cost as:



finally, the solution then comes to the greatest difference between these two curves:



Obviously, the optimum the above example can also be found using calculus. One would simply write equations for the benefit and costs functions and then subtract the cost function from the benefit. Since we are interested in finding a maximum, the next step is simple -- differentiate the B-C equation and then solve.

So, for the example above, the <u>Benefit equation</u> is for a straight line -- in the general form:

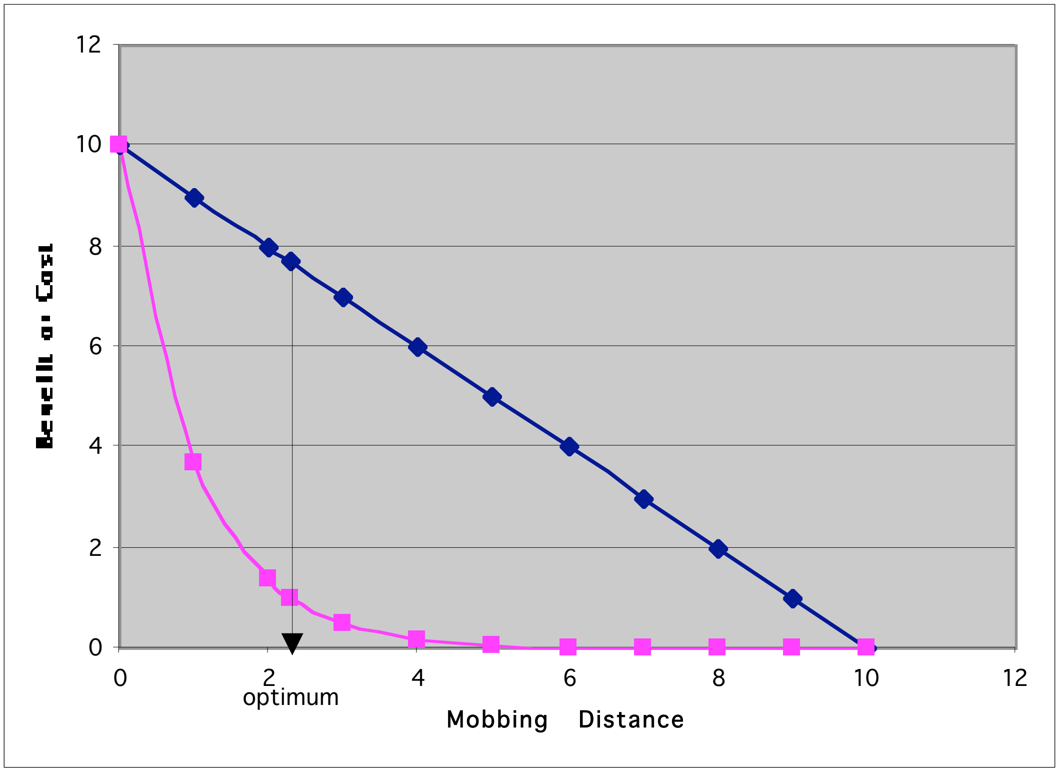
3. $B = k + ax$

where we will term distance "**x**" and we will assume that the slope "**a**" will normally have a negative value and the Y-intercept **k** will normally be positive.

The cost equation has the form of an exponential where ***r*** (the rate of change of cost with increase in distance) is negative (it is safer to mob from a distance) and ***j*** represents the cost of touching the predator

4. $C = j * e^{rx}$

Please go to the next page to see a plot of these two equations:



To find the equation for the difference in B vs. C over a range of mobbing distances, we **subtract eq. #4 from #3**

5. $(B - C) = Y = k + ax - j * e^{rx}$

(notice that since both C and B are in the same currency, we can just as easily define B-C as "Y"). We next differentiating each part with respect to distance (x)

6a. $$\frac{dY}{dx} = \frac{dk}{dx} + \frac{d(ax)}{dx} - \frac{d(je^{rx})}{dx}$$

Which solves as:

6b. $$\frac{dY}{dx} = 0 + a - jre^{rx} = a - jre^{rx}$$

<u>The greatest B-C will be given where the slope (dY/dx) of this equation equals zero</u>. So, setting this to zero and solving for the mobbing distance x when dY/dx = 0:

7a. $\mathbf{e^{rx} = a / (\mathit{j} * r)}$

7b. $$rx\ln(e) = \ln(\frac{a}{jr})$$

7c. $$x = \frac{1}{r}\ln(\frac{a}{kr})$$

Now, as an example, if <u>we assume that</u>:

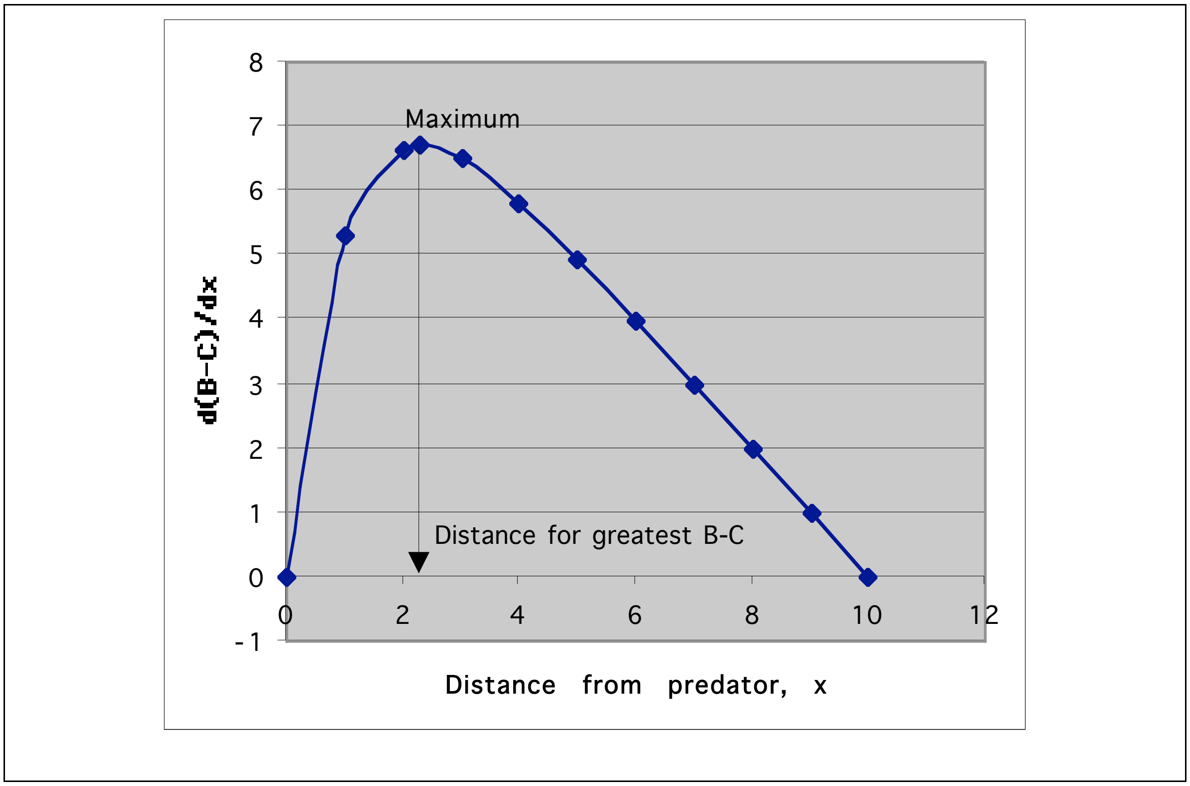
a = -1 (since the benefit plot as a negative slope with less benefit at greater distances between mobber and predator),

k = 5 (since the benefit was very high at close proximity between mobber and predator) and

r = -1 (this is just a rate constant for the decrease of cost as the predator gets further away); then:

x = 1 / (-1) ln (-1 / (10 * - 1) = - ln(0.1) = -(-2.303) = **+2.303 distance units**

Here is a graph of the equation #6b showing this maximum:



G. Example #2: WHELK DROPPING BEHAVIOR in crows.

1. Background: Fishing crows will often collect shell fish, fly up in the air, and drop them on shore side rocks in order to open them. Zach 1979 ("Behaviour" 68:106-117) studied such behavior using experiments informed by optimality theory. The questions he wanted to answer were:

(a) What is the best height for a crow to fly in order to open a whelk shell (a type of gastropod)?

(b) What are the factors that determine the best drop height?, and

(c) Do crows do what a thorough optimality model predicts? (Put another way, are crows behaving optimally, at least according to my model?)

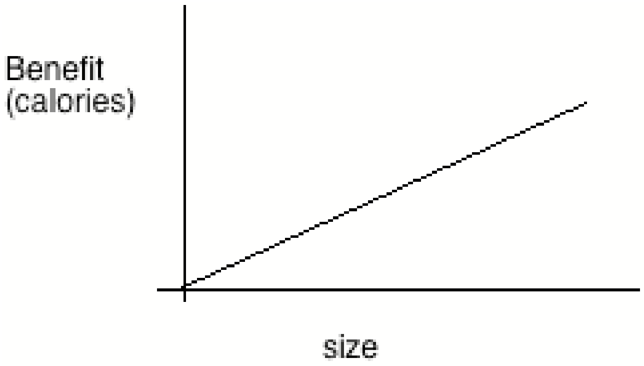
Important things to know:

- Crows only take the largest of whelks
- Flying straight up against gravity is, along with hovering, the most energetically expensive type of flight (since the wings cannot really support the animal in the way they do in more level flight and since gravity is being overcome constantly).

? Talk about flight in terms of costs and benefits. How about flights with the goal of dropping whelks? What are the costs and benefits and how are they measured?

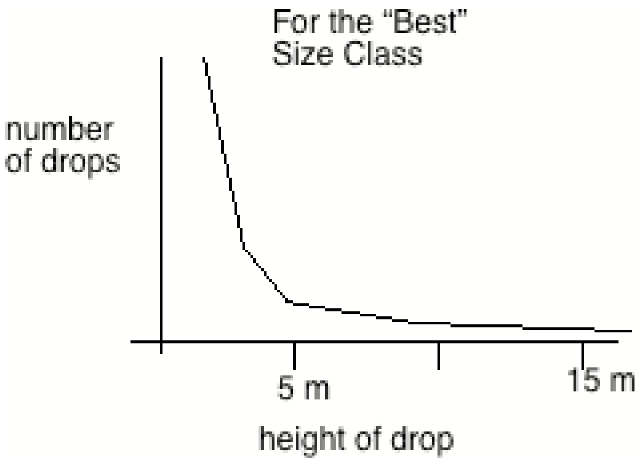
Now about dropping whelks: Consider the following: Not all whelks are the same size.
? Do you think there will be a relationship between the size of the whelk and the height from which it will need to be dropped?
? Can you imagine a reasonable relationship between size and payoff? Between size and cost?

Zach proceeded to **collect whelks of different sizes** and measure the available energy in them as compared to their weight.



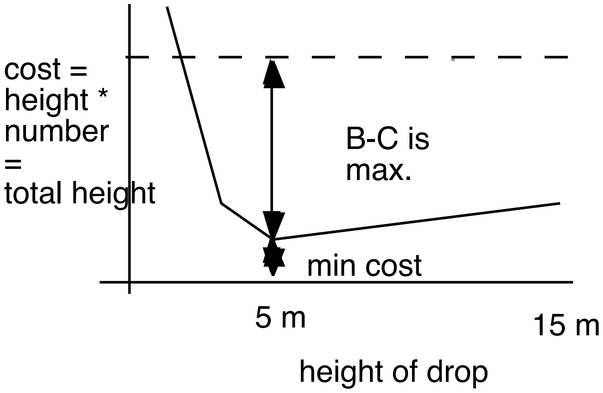
All the previous graph says is that per item, large whelks contain more energy than small ones. This rules out any large negative (or positive) allometry between weight and benefit.

What about costs? This is a bit more complicated. If we use energy as the currency, then costs are related to the number and height of flights: For any given size class of whelk the number of drops for a given height required to open the shell are shown in the next graph:



Cost = average # of drops * height
(energy = work * # repeats of work)

? What do you think such a curve should look like?
? How would you find the optimal drop height?
? What other factors might influence drop height?



crows pick a height that is
just slightly less than the optimum
-- perhaps to decrease chance of
losing
the morsal -- other factors may be
involved.

- The crows pick a height that is just a bit less than the predicted optimum.
- The results imply that the crow also considers certain other factors.
- Which size should it pick -- given a choice they will always pick the most profitable size -- the one that gives the greatest B-C.
- Below a certain size, they actually will go to other food since the payoff is less than the cost of opening.

H. Example #3: What is the best number of eggs to lay?

1. **ASSUMTIONS:** LIMITED ENERGY, MATERIALS AND TIME
2. TWO BIG QUESTIONS:
    - How does the animal "decide" **between REPRODUCTION** (reproductive effort, cost of reproduction) **vs GROWTH AND MAINTENANCE**
    - How are time, energy and materials divided between various offspring?

As in all optimality models, we will make trade offs. This will largely be a zero sum game, -- one can increase one factor only at the expense of another.

3. Decision variables: in the case we will study, it will be clutch (brood) size. But other studies would also be useful and they include that obviously are also related to fitness such as age-specific fecundity (how many offspring at different ages) and mortality rate; the related topic of longevity, parity (reproduce

just once or over many years), growth rate, offspring size, and the timing of breeding.

4. **<u>What is the optimal clutch size in birds</u> (or some other animal)? Work was done by Lack, Perrins and others.**

You should go back to the evolution/ecology review from earlier in the course and pull out the life history strategy notes before looking at this example (if you don't remember life history strategies). This problem essentially deals with life history parameter trade-offs in great tits and other birds.

Here is data from Perrins (1965) J Animal Ecol 34: 601 and 1979 **British Tits** New Naturalist Series

They deal with great tits (*Parus major*) -- birds that are in the same genus with our local black-capped chickadee and in fact greatly resemble the Massachusetts state bird!

A. Perrins, as others had before him, found that <u>great tits laid fewer eggs than they were capable of laying</u>. **<u>If you remove eggs they lay more</u>**. Moreover, **<u>they also seem perfectly capable of raising more young than they actually raise</u>** -- this was found out from **<u>fostering experiments</u>**

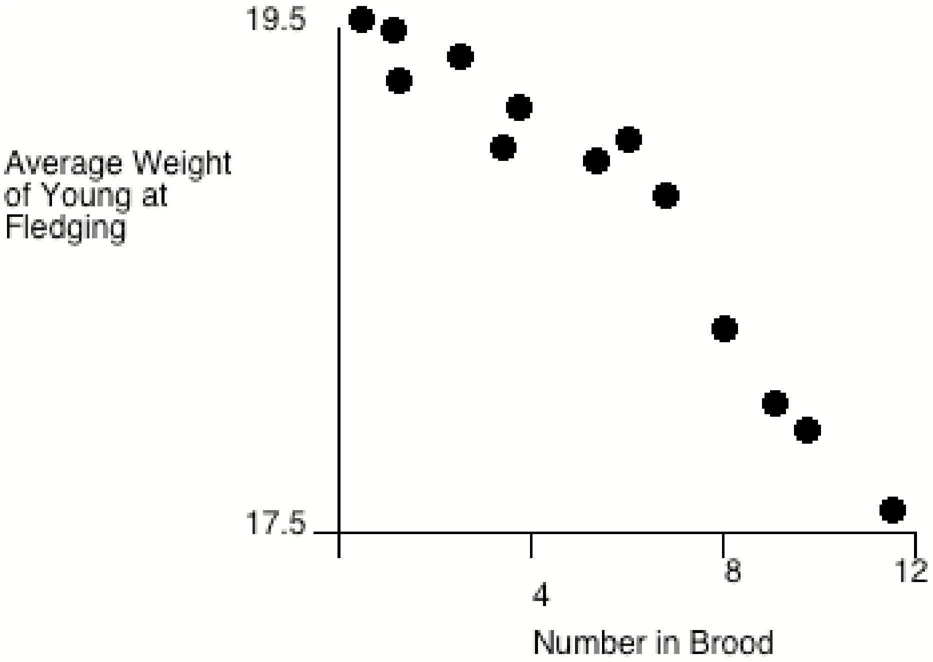
Why are these observations troubling?

There was also <u>variation in egg laying</u>. The number of eggs he found in different nests was essentially <u>normally distributed with a mean of about 8 and range of a bit less than 4 to a bit more than 12</u>.

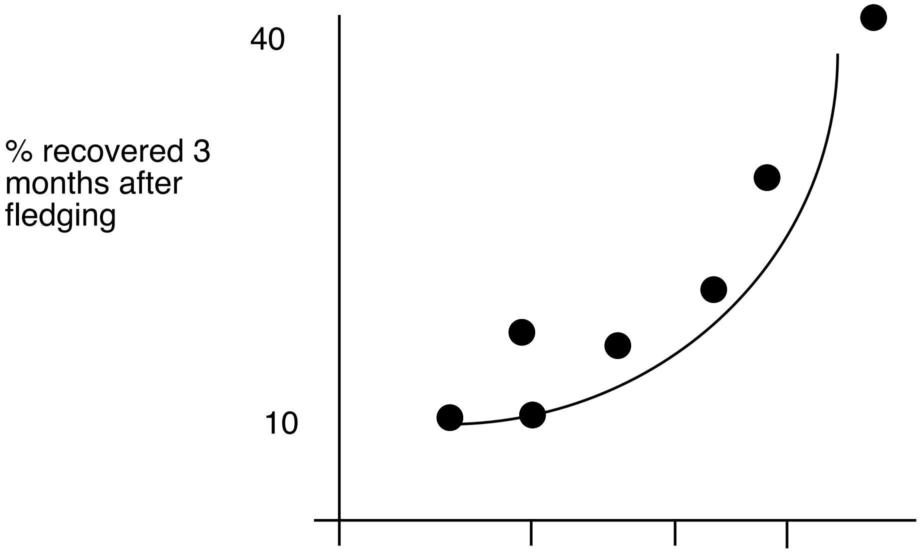
Why were they laying fewer eggs than they were capable of laying and fewer than they were capable of rearing? Perrins as Lack had before him, investigated this as a problem in optimality. What is the best number of eggs to lay? Here is will be a post hoc type approach since we already know how many eggs are laid and assume that selection has already optimized this. We want to see if we can predict the right number based a number of reasonable assumptions.

<u>Lack had suggested that perhaps part of the problem was that chicks do not do well in big nests</u>.

Perrins showed that **<u>weight at fledging was a function of clutch size</u>**:



He also found that weight was an advantage in survival:

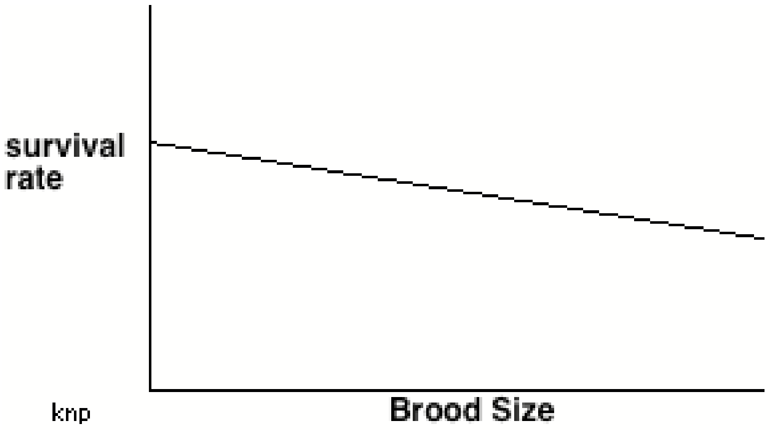


Notice that both of these graphs incorporate the bird's weight.

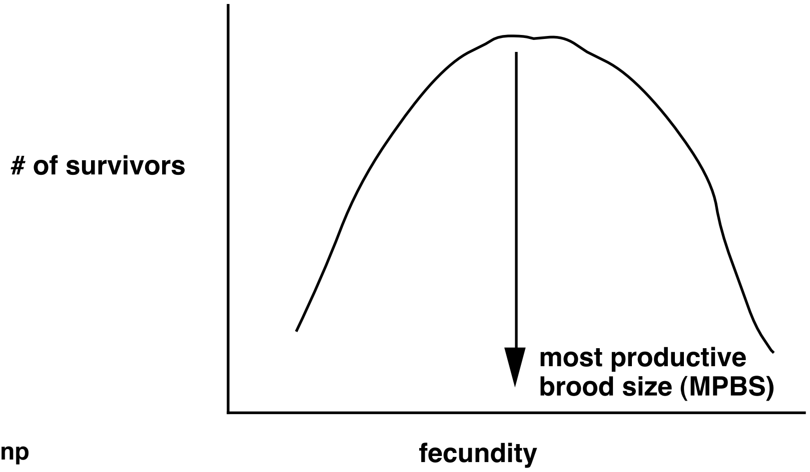
We can use the first graph to find the average fledging weight for broods of different sizes

Once we have the average fledging weight, we can use the second graph to find the % recovered after three months -- an estimate of general condition and, if we relate these data back to graph 1, an estimate of the chance that a bird from a certain size brood will survive.

A quick example of the calculation: From the top graph on the last page, if the brood size is 4, the average fledgling weighs about 19 g. If the broad size is 10, average fledglings weigh a bit under 18 g. From the lower graph on the last page we can see that about 25% of 19 g fledglings survive 6 months; that is, there is about a 25% survival rate for birds from a brood size of 4. Likewise, something less than 20% of the birds from large (10 bird) broods survive. The chance that a given bird will survive decreases with brood size:



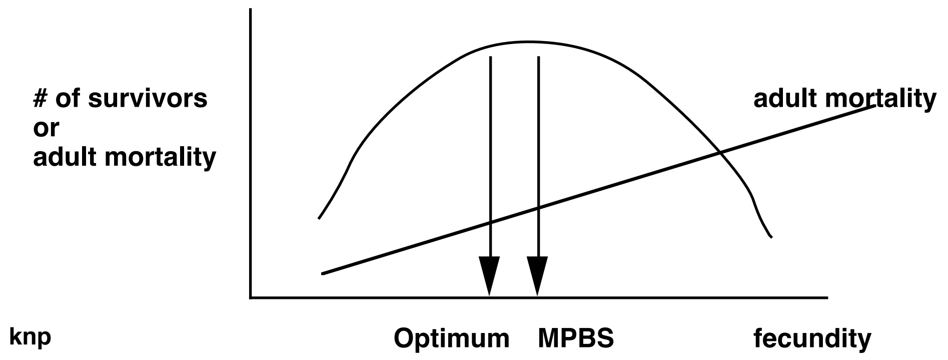
If we now multiply the brood size times the chance of surviving for six months when from a brood of that size we learn that:



and we define the optimum as peak of the curve that is referred to as the **most productive brood size (MPBS)**. **<u>This is the brood size that gives the greatest number of successful offspring.</u>**

Notice that in this particular model the final product (the graph above) has already essentially taken into account the differences in costs and benefits. It did this with the survival function that took into account the cost of increased brood size on reproduction.

To test this model, one simply goes to the field and finds the average brood size. In fact, the average brood size is slightly less than the MPBS! So, the model needs some modification. Further work by Perrins showed that the larger the brood size, the greater the chance that a parent bird would die before the next year. In other words, the bird could trade lots of young now for a lower chance of survival and reproduction next year! Using life tables (kind of like what insurance agents use to estimate premiums) he could estimate the **<u>future reproductive cost</u>** to a bird if it dies before next year. If this was multiplied times the chance of dying as a function of brood size, the result was lost future offspring as a function of present brood size. This was then combined with the model we just saw:



Clearly the result is that the optimum is lower than the MPBS -- reproducing a bit less is better for the long run (in most cases at least) and results in an overall higher reproduction. Thus, the optimum is a bit less then the MPBS.

Notice that this optimum could be solved for using general equations for a straight line and a "reverse parabola" – solving for the difference using calculus to obtain a general equation that could then be solved for the specific constants found in a certain situation (see earlier box in these notes on solution of problems like this).

I. Rate Maximizing Models:

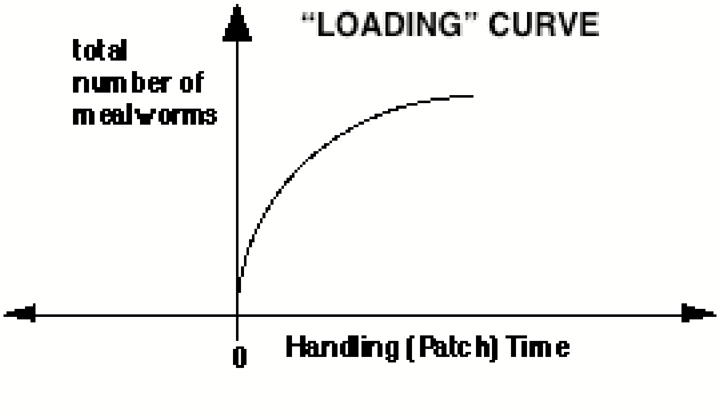
1. Let's return briefly to Zach's crows. Recall that Zack saw the crow's problem as simply deciding how high to drop a particular sized welk so that the net gain per welk was maximized. We didn't worry about how long it took or more precisely, how much was gained per time. This is fine, but one meal will

not keep an animal going. In the example below, we will see a situation where both time and net gain are crucial and what is being maximized is the **rate, not B-C** .

One could argue that in the brood size optimization questions that time was factored in since it was offspring per clutch and it was assumed that there was generally only one clutch per year. However, time is a trivial variable in this case since it does differ between individuals -- it is not a factor related to phenotypic variation.

2. **Construction of a Rate Maximization Model**: Suppose that a bird needs to fly from its nest to a foraging patch where it then spends more time looking for food. Notice that in the trip the bird is paying a cost that could be measured in time, distance, energy or even risk with all of these variables supposedly increasing for longer trips. When the bird arrives at a foraging area it will also spend a certain amount of time there. However, as it removes food, more food becomes harder to find since it has depleted the patch where it was searching. It may also have more trouble carrying the food as the load gets larger. So, how long should it stay on the foraging patch? Modeling this problem requires a number of steps:

a. Construction of a "Loading Curve": Let's review what happens when an animal arrives on a **patch** to forage (or whatever). In the case of foraging, the longer one spends on a patch, we assume the greater the reward. But does that go on forever? Obviously not. The patch may well become depleted and so the forager may have to look longer for each prey item. Or, if the forager must carry the prey back to, for example a nest , it may have increasing difficulty holding the prey the more it has obtained. Think about yourself trying to carry too many things at once. Here is a typical **patch time** or **loading curve** for the situations just discussed:

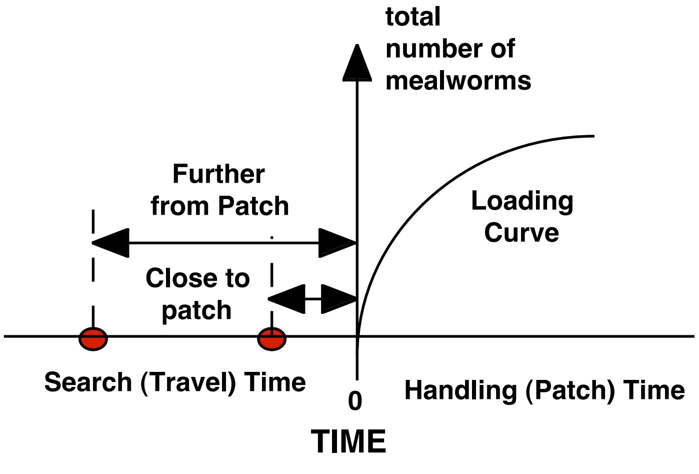


the axes are some measure of benefit (for instance, meal worms taken in the example above) vs. time spent on the patch. Imagine the origin of the graph as being the point in time when the animal arrives at the patch. Thus, the loading curve describes the average relationship between patch time and reward.

Could there be other shaped loading curves? The answer is yes -- imagine a few reasonable ones and give a scenario for each.

b. Search time or transit time. The crow must fly **back and forth** from its nest to the foraging **patch**. We assume (and in fact we know) that birds take the most direct route feasible to the foraging patch. Thus, the travel time (usually called **search time** since the animals must often locate a new patch on each trip) is a function of distance and in the simplest cases where a patch is resample by the same bird, the distance is definitely related to time. ***Note that we always include the return trip time in the search time even though it is often different than the "out trip" time.***

We visualize the search **travel time as distance to the left of the origin of the graph** -- *i.e.*, as being the time taken in getting to and returning to the patch. Since patch time is to the right of the origin, travel time must be to the left. The further to the left, the further the distance from the patch (or the harder it is to find a patch). Note that negative numbers are not used on the time axis. Instead, the center (where the currency axis emerges) is seen as time zero and time is added going both directions from this origin. Thus, the graphs origin can be seen as the arrival on a foraging patch.



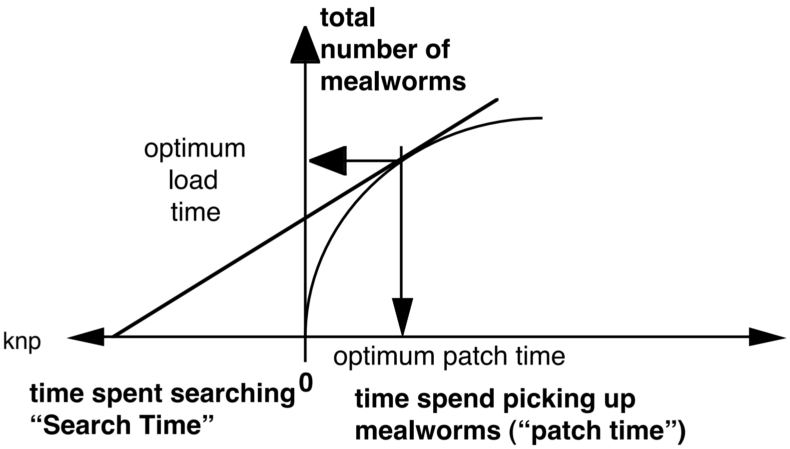
So if you leave from a particular place (such as a nest) and travel to a patch taking a given amount of search time, how long should you spend on a patch so as to maximize the rate of food intake (mealworms/time or calories / time)? First realize that the total time, called the foraging (handling) time

8. foraging (handling) time = trip + patch time

is the time used to calculate the rate of return.

Think of the search time as a constant, $\mathbf{t_s}$ **,** for a given trip. It cannot be made larger or smaller.
On the other hand, the rate of collecting resources can be maximized by collecting more food items per trip and/or by minimizing the time spent on the foraging patch.
What happens if you simply stay on the patch so long that you cannot carry any more food or you totally deplete the patch? To do this will take a long time (look at the loading curve). Recall that the loading curve is one of diminishing returns. If one stays this long and maximizes the gain, unfortunately, time is also maximized since patch time is as large as it could be. When added to the search time, the rate becomes low.
Likewise, very short patch times will yield very little benefit. So, although time will be minimized, so will benefit and the rate will be low.

c. Now, since the loading curve describes the typical time course for obtaining resources (here mealworms per time), the solution will have to involve points on that loading curve. Which point gives the greatest **<u>rate of payoff</u>** <u>GIVEN THE TRANSIT TIME</u>? The answer is a **<u>line drawn from the start point (nest) that is tangent to the loading curve</u>**:



total handling time

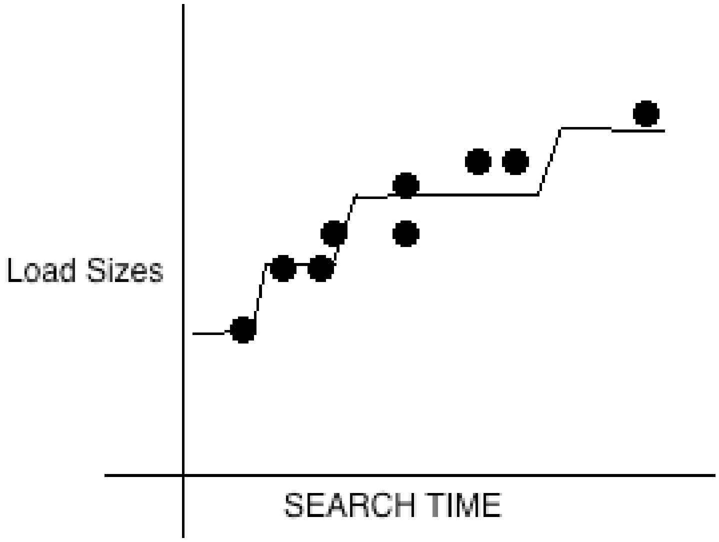
Notice that time rates have been maximized in the model we just (and will consider). However, there are cases where other types of rates might be maximized -- for example, if the x-axis were fight risk to a male seeking mates and the Y-axis was mating opportunities.

d. Testing Rate Maximization Models: Kacelnik 1984 J Anim Ecol 53-283-99 and starlings and "leatherjackets".

(i) Experimental Design Kacelnik wanted to see if crows were rate maximizers when foraging for beetle larvae that are like mealworms and are called leatherjackets. To perform this experiment,

- he created artificial patches that were feeding boxes with potting soil and leatherjackets. He could therefore easily vary the "load" or richness of each patch by putting in fewer or more larvae.
- Banded crows (therefore individually identified) were trained to identify these boxes (they are very smart animals) and the times between when they left their nests and arrived at a given foraging box was known.
- The search time could be varied by moving the foraging box around. The load taken and patch time was easily measured by observing the birds on the foraging patch.

(ii) Results plotting load size vs. total trip time. Each point represents the result for one bird on a patch. The **line represents the predicted load sizes for various distances between foraging boxes and nests (search times)**. This was derived from his optimality model and was based on his experimental measurements of loading curves. Note that in this graph that total time was not used here (it could have been) but this variable is closely related to load size and so need not be included. The fit was excellent:



Does it make sense that longer search times should be associated with longer patch times and larger loads? Explain in terms of what is being maximized. Using the loading curves you imagined earlier in this section, find the rate maximizing optima for two travel times each.

II. CRITICISMS OF THE OPTIMALITY CONCEPT:

A. There have been a number of attacks on the idea of optimality.

1. These should have the effect of making you understand some of the limitations of the concepts and some of the dangers that can befall the uncritical. There have been problems when individuals have tried to take the concept too literally -- for instance, many have assumed that some organisms or even populations are fully optimized for some characteristic and not that they just approach an optimum.

2. Furthermore, there has been a tendency to overlook other explanations for the characteristics organisms have -- optimality theorists have tended to assume that any characteristic represents an optimum without actually showing that these were "optimum".

3. Finally, it is vital that you keep these criticisms in mind anytime you are considering a problem related to how some trait has evolved. They represent areas where many very good scientists have made embarrassing errors when they have not carefully considered the many factors involved in evolution. If you spend the time to carefully reflect on these critiques, your understanding of evolution should be greatly deepened.

4. Some of these critiques also have political overtone to them. Some individuals oppose giving natural selection credit for everything (and certainly don't like the political implications of that view).

Note: we will use the term "strict optimum" to refer to a trait that actually represents the best possible B-C and not something that simply approaches the best B-C.

B. Arguments against the occurrence of strict optima based on the nature of the genetic system

1. **Mutation** -- no population could remain at an optimum since there is always mutation -- any net mutation of alleles away from the form that causes the optimum will result in the population moving away from the optimum. However, mutation rates are low and therefore we would expect that any pushing away from optimum as the result of mutation would result in only a small departure.

b. Genetic Linkage

1. recall that alleles of loci that are located physically near each other are said to be **tightly linked**, this means simply that they are not likely to be separated from each other as a result of crossing over.

2. thus, image that two loci are adjacent and that on one chromosome one of the loci possesses an advantageous allele while the other is deleterious

3. the chance that the linkage will be broken down by a crossover with the other chromosome is very low; thus it is likely that the loci with the "bad" and "good" alleles will remain linked together.

4. selection sees the overall phenotype and not single alleles -- thus, as long as the effect of the locus with the bad allele is not too bad, the organism will survive but it will not be optimal and it will have a hard time getting to the optimum suggested by the locus with the "good" allele.

c. Pleiotropy --

1. in this case the point is that many alleles are pleiotropic -- that they affect several aspects of an individual's fitness. It is quite possible that something that affects fitness positively in one way (such as the way studied by the optimality investigator) also has a deleterious affect in another way.

2. A well-known example of this would have to do with exaggerated secondary sexual characteristics in the males of some species.

a. such characteristics increase the attractiveness of these individuals to females; they are useful in sexual selection competitions.

b. however, the same structures may not only make their possessors more visible to predators but may also inhibit their ability to escape, thus lowering their fitness through natural selection.

3. so the point is that the structures can be seen as optimal only if viewed in terms sexual selection but not as survival promoting.

d. Co-adaptedness of the gene pool vs. treating genes as if they are in isolation ("bean bag" genetics)

1. Genes form an important part of each other's environment. Gene's must be able to work with each other or at least not badly get in each other's way. This should be obvious when you consider that not only must the products of genes (proteins) interact to produce functional pathways, but also the products and needs of separate pathways cannot conflict in such a manner as to produce an organism that does not function in a manner that allows it to reproduce.

2. We often speak therefore of the need for the alleles at various loci to be adapted to each other, that is, **CO-ADAPTED** and therefore to form a **CO-ADAPTED GENE POOL** within the organism and in the species gene pool as a whole.

a. this does not imply that we believe that all alleles at all loci will be perfectly adapted to work with each other -- there will be all degrees of co-adaptedness

b. it does mean however, that alleles that really cause others a problem will be selected against.

3. optimality models often seem to imply that loci are free to evolve on their own as long as the result maximizes B-C. The critics warn that alleles must be able to work with others and therefore the ones that produce the best possible solution for some narrow problem might not necessarily blend well with others with the result that the optimal solution is not possible to achieve in these cases.

e. "Sisyphean" genotypes -- the reshuffling due to sex

1. Sisyphus was condemned to, for eternity, to roll a large rock to the top of a hill, each time only to have it roll back down again. Thus, the task was never completed.

2. Sexual reproduction is analogous to this -- assume that briefly an optimal genotype is achieved -- the equivalent of getting the rock to the top of the hill. However, due to the nature of sexual reproduction, every genotype is broken up during gametogenesis and then syngamy. Sexual reproduction's purpose is to generate as many different combinations as possible at random, thus the optimum is lost each time (although it will be nearly approximated in the next generation -- Why?

f. Maintenance of diversity -- balanced polymorphisms;

1. In certain common environments, many loci require heterozygosity to produce the most fit phenotype. One of many such examples is sickle-cell anemia, when in areas where malaria occurs individuals who are heterozygous for sickle cell anemia are more fit than either homozygote. Such a system, where the heterozygote is more fit than either of the homozygotes (either or both of which may in fact even be lethal!(but they don't need to be)) is called a **BALANCED POLYMORPHISM**.

2. While the heterozygote may be very fit, the price that is paid is that the two homozygotes are less fit. Thus , 50% of the offspring of a cross between two individuals that are heterozygous are noticeably less fit than are their parents.

3. Anytime this sort of situation exists, the price for optimality in certain individuals is very low fitness in some of their offspring. Thus, the effects on the population are such that we would be hard pressed to define the solution as optimal compared to what could be easily imagined.

! Notice the lack of morality and fairness about this. Unfortunately, evolution simply discovers solutions that work for their possessors and make them more fit than those they are competing with -- it does not guarantee that all offspring will benefit, instead only that more will benefit than is true from other parents.

B. Phylogenetic Inertia -- "You can't get there from here"

1. It may not be possible to actually achieve an optimal solution because of what is termed phylogenetic inertia. This is closely related to several of the reasons that we have already discussed, here the idea is that organisms have a certain evolutionary history, a certain co-adaptive gene pool and only certain of all possible alleles (by definition, any species contains only a subset of all of the different alleles that exist at any one time)

2. Thus, the organism goes from where it is to the closest it can get to an optimal solution. And obviously, given the different evolutionary histories of different organisms, so-called optimal solutions to a common problem might converge but they will not all exactly be the same -- wings have evolved in vertebrates three times and they are aerodynamically similar but they are certainly not identical structures and must be used slightly differently to achieve good flight. And no wing is perfect for all types of flight that an animal might conceivably need to do.

C. Arguments against the occurrence of strict optima based on the nature of the ENVIRONMENT

1. There are two related phenomena at work here -- **environmental heterogeneity (both spatial and temporal variation in the environment)** and **evolutionary lag**.

a. **environmental heterogeneity** implies that since the environment differs in different places at one time and over time, no single organism can possibly hope to be optimally adapted to every place it might reasonably find itself nor if it is adapted now should it be certain to remain so.

b. **evolutionary lag:** is part of the reason above, this term simply points out that populations are most adapted to the previous environments (except under extremely fortuitous and rather rare circumstances). Thus, we should not be surprised and nor should be expect to find that animals are optimally adapted to the present environment.

2. These are some of the most powerful reasons to never expect perfect optimality except in very stable environments.

D. Arguments against the occurrence of strict optima based on the occurrence of random events in evolution:

1. Structures in place by random and neutrally-adaptive events represent the starting place and to some degree a constraint on evolution and therefore the attainment of an optimal solution:

2. We know that many if not all structures or behaviors owe part of their exact phenotype to various types of accidents -- for instance founder effects, genetic drift events that once occurred.

3. The result of these events was that these organisms represented a new starting point for future adaptive evolution.

4. Recall that adaptations (and therefore optimalities) involve approaching some ideal solution to a problem (for instance, how to flap a wing or allocate reproduction among members of a society).

5. Recall also that since evolution works by tinkering with what is already there (no matter how it got there) to find solutions that work well enough

6. Therefore, given these different starting points and limitations inherent in them, we would not normally expect to see a perfect adaptation -- just one that works quite well.

E. Arguments against the occurrence of strict optima <u>based on sloppy science or our misinterpretations of what we see or problems of bad explanation:</u>

1. **<u>Panglossian Explanations and the Spandrels of San Marco</u>** (SJ Gould):

a. In Voltaire's *Candide* Dr. Pangloss was a character who interpreted everything, even the most inhuman outrages as for the best and thought that we were living in the best of all possible worlds. **<u>Panglossism</u>** is a term applied to the tendency to see all structures that an animal has as the best possible -- the way I have heard this argument made by some good biologists is that "we know that natural selection occurs and it is a powerful force, therefore it must result in adaptations that are optimal, even if they don't appear to be to us".

? Defend and attack this argument. Does it seem to be a reasonable approach to take logically? Try to see it both ways.

b. **<u>The Spandrels of San Marcos</u>** refer to an observation made by Gould and Lewontin based on the San Marco Cathedral in Venice. Spandrels are flat panels that are needed to help put a dome on supporting architecture. In San Marco they are highly decorated, yet they are obviously not the reason or goal of San Marco nor does the decoration represent an optimization of their actual function. Put another way, the existence of a trait does not prove its adaptive value. We have already seen this when we looked at the trait of kidney size and asked whether large size was what was adaptive.

2. "**<u>Just so" stories</u>**:

a. Rudyard Kipling wrote a series of stories most of us know called Just So Stories that fancifully explained how elephants got their skin along with a number of other characteristics of animals.

b. The technique used is to start with the present (end point of evolution) and then make a series of causal conjectures as to what happened to get things to where they are at present.

c. It is important to avoid the construction of reasonable stories that are nothing more than conjecture without having some way to test them -- and short of a test, it is very important not to make much of these arguments no matter how pretty or pleasing they are -- they are little better than the biological version of Just-So Stories until considerable experimental evidence is gathered on their behalf (they have not been disproven while reasonable alternatives have been knocked down).

d. It is especially a problem in sociobiology and evolutionary biology because it is:

1. the studies often take a very long time to complete and therefore pretty ideas can be talked about a lot in the meanwhile and become part of the scientific and popular culture

2. there is a tendency to generalize about behavior from humans to animals and vice versa without a lot of evidence -- these speculations are very interesting to us and we often forget that they are nothing more than speculations.

! Just So Stories are among the most important criticisms both of optimality and they ways that evolutionary studies should be and are conducted. Be sure you understand this one.

? What is the usefulness of optimality? Should we be talking about a single trait or many? Optimal for all environments or just one?