Bio 45 – Lect. II-2- Basic Concepts of Optimality Theory

I. Organismal Economics - Conceptual Basis for cost/benefit thinking (from previous handout)

A. Design and Cost/Benefit thinking.

1. Any trait involves a set of costs and a set of benefits. The costs include energetic costs for producing and maintaining it as well as the constraints it puts on other aspects of the individual's phenotype and thus its overall fitness. The benefits are gains to an organisms' relative fitness due to having the trait. Thus the **net advantage** of any trait is the fitness **benefit** of that trait **minus** the **costs** to fitness of having the trait. Since costs include things like risk, they are often hard to measure – especially if costs and gains must ultimately be converted to units of relative fitness. Thus we tend to use a variety of proxies for fitness – proxies we can relate to fitness and yet more easily estimate or measure. The most important proxies are time and energy.

B. Time and Energy Budgets

1. Animals have a finite amount of time and energy during their lifetime (or at a critical period during it). They use this energy for: **Growth** (e.g., building muscle or getting big), **Reproduction** (e.g., competing for mates or making & caring for offspring), and **Maintenance** (e.g., finding & catching food, avoiding predators, or repairing damage)
2. Since total energy (time) is allocated among these three, any increase in one means the others must decrease. The "goal" is to maximize survival and reproduction relative to others. Those animals that obtain and allocate energy (time) most profitably while minimizing costs and risk will be favored by selection. The long-term result should be optimal energy budgeting (maximized "profit").
3. Time and energy are often interchangeable units– time is energy physiologically. Since we are most interested in the relative fitness of individuals with different traits, we can substitute time for energy. For example, suppose there is a basic cost (in calories) per minute of flight for bumblebees. Then two bees that differ in how long they fly before finding nectar will differ in the costs of foraging. To compare them we need only assume they have the same calorie per minute of flight costs and use the time they spend flying as the estimate of their costs.

B. Three caveats about using cost/benefit thinking – more details later

1. Our models do not directly test the theory of evolution by natural selection. We take it as a given. However, if we cannot make models and predictions based on this assumption that work, then we have to deal with the possibility that our assumption is wrong.
2. The best solution (design) is not necessarily the absolute best. It is, given the given specific conditions (the problem), whichever of the alternatives available works best. Remember: the best available alternative for a given set of conditions, not the best of all possible alternatives.
3. We assume that Energy and time are good currencies to use to predict long-term reproductive success or fitness. We will look at this in more detail

II. General Comments about Models and Optimality Models

Optimality modeling is a formalized way of cost/benefit thinking. We assume an ongoing evolutionary competition among different types of individuals in populations. Over time those designs that are most efficient at extracting resources from the environment and turning them into offspring with a high chance of survival will become more numerous and persist until replaced by more efficient designs.

Our models, based on this view of selection optimizing design, could fail to make correct predictions about organisms. If so, have we (1) made an error in our basic reasoning, (2) overlooked some basic constraints on the organisms that keep them from optimizing, or (3) failed to see a better way to do it -- one these animals have evolved instead? Of course the failure may mean that selection does not work the way we think it does. Thus we can learn about the role of selection in the evolution of behavior by producing these models and testing them and refining them.

Alcock (see index) introduces some of the basic concepts of optimal foraging theory and provides some examples. Below I introduce the essential elements of optimality models. I will illustrate these in lecture using simple optimal foraging models and you will examine other foraging models and tests of them in discussion section and in your journals.

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Rules of Optimality Modeling:

Since we cannot expect all organisms to have reached the best designs possible, how can we study optimal design? Essentially we are going to focus our efforts on a formalized set of rules for building and testing models of how we expect animals to be designed and for refining these models if they do not work. This process will help us understand how things actually do work. The formalized procedure helps us avoid making mistakes by keeping all of our assumptions and guesses out in the open for others to examine, criticize and modify. The result is a quantitative, evolutionary way of asking "how" questions -- how should it be designed? You need to know the basic language and structure of optimality theory described below.

First we define the **currency** to be used. Ideally it would be "units of fitness"; but that is hard to do. Instead we usually use **time and energy**. These can be measured fairly easily and can be reasonably linked to fitness. The connection between time and energy and fitness comes from our conceptual understanding of the energy budget discussed above.

Second we define a **utility function** -- the thing to be maximized. Those animals that come closest to maximizing the utility function will gain fitness relative to their competitors. A typical utility function (energy maximization) might be calories gained per calorie expended (a measure of profit made in obtaining energy). Another (time minimization) might set a goal of calories gathered and minimize the time taken to gather them.

Third we identify the **problem to be solved** or, if you like, the exact nature of the contest between competing individuals (competing to maximize relative fitness). For example, what might be the best way to determine when to abandon one food patch and search for another in a given environment, or it might be the number of items to carry back to a nest from different distances away from the nest.

Fourth, we define the **constraints** on the organisms and thus on our expectations. Often these are given as **assumptions**. For example, simple diet choice models assume that the forager can recognize the same prey differences we can (the ones we will manipulate to test our models) and can rank prey on the basis of their net caloric values (energy received minus energy spent catching and eating the food).

Finally, we **produce our model and devise ways to test it**. Usually we develop a simple model that gives the best solution for the utility function. We then set up laboratory or field conditions so that we can directly test whether our models work. One way to do that is to derive predictions from our model -- what should animals using such a model be expected to do? We expect a definite predicted pattern of behavior from our models (choose only those prey types that exceed a certain gain/cost ratio, for example). Usually our predictions are tested against a **null hypothesis** -- what randomly foraging animals should do. Thus if we collect the data and the pattern is no different from random choice, our model is in trouble. Note that the null hypothesis forces us into a strong test.

If the model doesn't work (make the right predictions) we have several options. First we could toss it and try a different one. Second, we could look closely at our model and its assumptions. Are we expecting too much of our animals? Were some of our assumptions are wrong? Can we adjust the model so that our assumption is more reasonable? We can then **make adjustments and test** the new model with some new experiments.

Remember that the process of proposing and testing and revising models has two goals: 1) How close can we come to accurately predicting the behavior of animals and 2) how general can we make these predictions? The second -- general model -- goal is prized because it uncovers and helps explain a basic, widely shared design. We expect general behavioral designs since there are many examples of shared biochemical, morphological and physiological traits throughout the animal kingdom. Some of these reflect shared ancestry (homology -- successful traits passed on from common ancestors) and some reflect the fact that at times there may be only one best way to accomplish something such that any animal doing it should do it a certain way (convergence). However, one thing you will learn from this course is that a search for THE answer is likely to get us in trouble. How one deals with "wanting" general answers and not getting them is part of learning how science is really done.