EVOLUTIONARY ECOLOGY
ZOOL 5133 - FOX

OPTIMAL FORAGING

All models of optimal foraging entail an economic appraisal of costs vs. benefits associated with the harvest of food. Large prey/small prey, easy prey/difficult prey, nutritious prey/junk prey--all have specific costs and benefits. The ultimate benefit is the energy contained in the food. The ultimate cost is the energy expended to harvest the food. Few models incorporate other costs like risk of predation or territorial intrusion during the harvest of food; most are an economic balance of calories in, calories out. This laboratory will test a few predictions of a simple, graphical model of foraging behavior developed by MacArthur and Pianka (1966)-- a model that anticipated much of the current theory of optimal foraging. Its greatest value is its simple introduction to the rudiments of optimal foraging. You may feel it worthwhile to review the original paper; certainly look over your pertinent lecture notes and the pages of your text (Pianka 2000:284-287) that summarize the MacArthur-Pianka model before coming to lab.

The MacArthur-Pianka model, like subsequent ones, is an economic cost/benefit model of optimal foraging. But it considers only time, not energy. The optimal diet is the one that minimizes the time per capture of each prey item. The economic (really, evolutionary) optimization is diet size: should an animal eat only prey A and B, or should it eat A, B, and C? As conditions change (e.g. food abundance falls) how should its diet size change? These questions (and more!) can be answered by analysis of the benefit (as decreased time/prey captured) and the cost (as increased time/prey captured) associated with the enlargement of the diet from N to N+1 (or, as above, from A, B to A, B, C). Prey are first ranked from easiest to catch to hardest, or really from least time-consuming to most. The diet size is indicated on the abscissa: 1 type; 1 and 2 types; 1, 2, and 3 types; 1, 2, 3, and 4 types; etc. The ordinate scales the DECREASE in search time/prey captured (S) as the forager expands its diet from N to N+1, and also the INCREASE in pursuit time/prey captured (P) with the same dietary expansion. One can see by inspection that the diet should be enlarged as long as the benefit/prey captured exceeds the cost/prey captured, or as long as the S curve is higher than the P curve. The intersection of the two curves indicates the optimal diet size.

Extending this basic model, one can predict changes in diet size as food abundance changes, or as foragers with low vs. high S/P ratios encounter altered food abundance. Other ramifications can be considered.

This lab will test the basic theorem of the model, the effect of altered food abundance, and the differential response of foragers with different S/P ratios.

Materials:

Colored toothpicks or the like (5 colors). A large (1000 m^2) outdoor foraging area, wristwatches, or preferably stopwatches, a few baggies, and sharp eyes.

Methods:

One can pretend we are all little birds feeding on even littler bugs and spiders. The five colors of picks represent 5 species of prey. The optimal diet is that which minimizes the time used to collect (find and capture) the prey items.

Black	5 seconds
Red	10 seconds
Blue	20 seconds
Green	40 seconds
Brown	80 seconds

The P curve can be calculated from these data: The items are ranked from easiest to hardest to catch as above. If one bird phenotype forages only for the first (black), its P_1 value is 5 sec/item. If another phenotype forages for the first and the second (black and red)--and all prey are equally abundant--then it will pursue black picks as often as red, so P_2 is (5 + 10)/2, or 7.5 sec/item. The other P values for larger diets can be calculated in like manner. Now we need to plot P, not P, against diet size: P for diet of 1 prey species is P for 2 diet size minus P for 1 diet size. That is, the INCREASE in pursuit time/item captured from a diet of N to N+1. That increase is plotted from the ordinate above the diet value N+1. The other P values are plotted likewise and connected by a smooth curve.

The S curve must be obtained empirically. Sprinkle the 5 colors of picks over the foraging area. Specify the diet of each bird. Let the birds forage for their diet over 5 minutes. Utilize a pursuit time of zero for all colors. For each diet, divide 5 X 60 seconds by number of total picks collected to obtain S_N, time per item found. Average values of diets replicated by two or more birds. In a fashion parallel to the calculation of P for each diet size calculate S for each diet size. Plot this DECREASE in search time against increasing diet size: $S_N = S_{N+1} - S_N$. Again connect the points with a smooth curve. The intersection of the two curves denotes the optimal diet size. It is tested below.

Basic theorem of model: Scatter picks as before. Assign diets and pursuit times to each bird. Allow birds to forage for 5 minutes, now using appropriate pursuit times. Calculate optimal diet size from minimal time per item eaten (maximal number per 5 minutes). Compare to model.

Increased food abundance: Scatter food at double the density as before. Allow birds to forage for 5 minutes as before, again using appropriate pursuit times. Calculate optimal diet as before. Compare results to model and to previous results.

Low S/P vs. high S/P: Scatter food again at double density. Allow birds to forage 5 minutes using appropriate pursuit times, but with doubled search time abilities: each bird ignores every other pick spotted, so in effect, these birds show a S/P ratio double that of before (P is unchanged). This is the high S/P group. Use results from before (a.k.a. the low S/P group) to compare performance following an increase in food abundance. Compare results to model and to previous results.

In each case plot the S and P curves against diet size. Discuss the fit to the model and, most importantly, the direction of change in diet size (generalize or specialize) following a change of conditions. MacArthur and Pianka (1966) claimed that the greatest utility of their model lay, not in a precise prediction of diet for a forager, but rather in a comparative prediction of diet change following a change of conditions. Why is that?

Recheck of S curve: If time permits, recheck the S values for different-sized diets under pursuit times of zero. The birds may have improved their pick-spotting ability (or the reverse, as the lab drags on). Relate such a change to the empirical fit of the model.

References:

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

Pianka, E. R. 2000. *Evolutionary Ecology*. Harper and Row, NY. (6th edition).