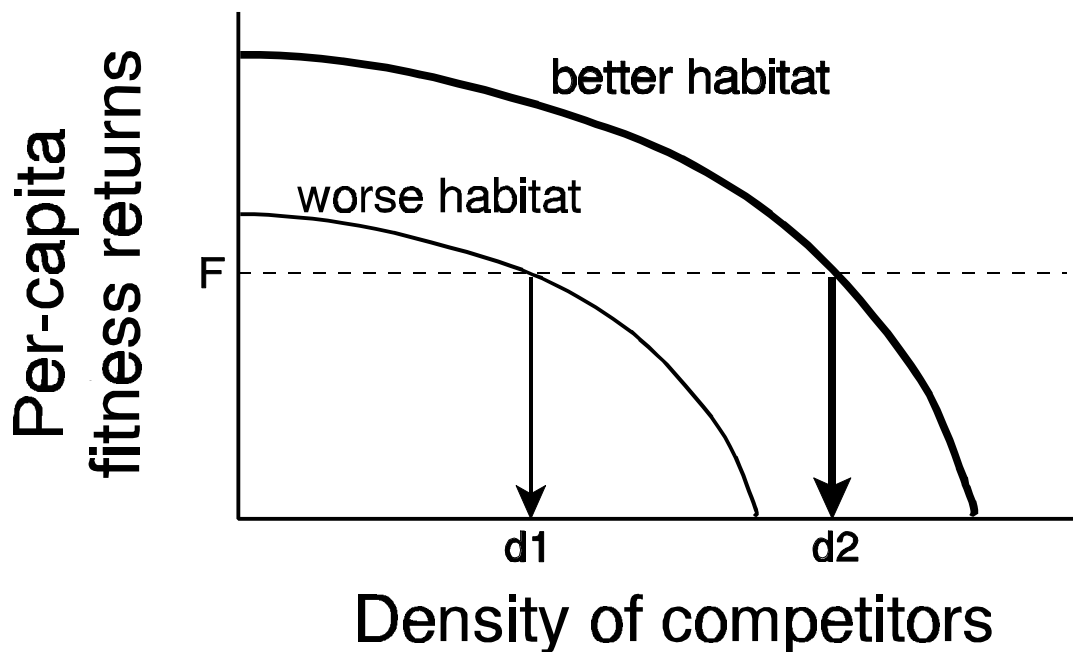


### Seven Swans A-Swimming: testing ideal distributions

Behavioral ecology postulates that organisms make adaptive behavioral choices. One of the common problems they face is a choice between different places to feed, mate, nest, rest, etc. Unlike many simple diet-choice problems in foraging theory, many of these 'patch' choices are strongly affected by the presence of competing animals. A patch may be a discrete area of interest, such as a feeding site, or much larger, such as an entire habitat type. Stephen Fretwell in the early 70's came up a novel idea to predict how animals should distribute themselves across patches that differ in fitness payoffs, given that competition lowers the payoff in each patch. His insight was that animals that were **free** to make choices between patches should **ideally** move between them until they could not increase their fitness any further. This distribution is called the 'ideal-free' distribution. Coupled with the depression in fitness returns as the density in a patch increased, this principle leads to several predictions: 1) there should be more individuals in better patches than worse ones; 2) the fitness gains of all individuals in all patches should be identical (within measurement error). These predictions can be demonstrated graphically:

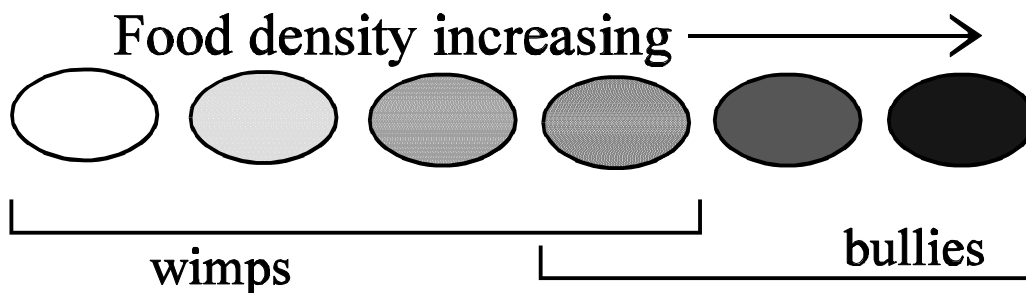


In this graph, there is a total of  $(d_1+d_2)$  animals looking for food, mates, etc. In the ideal-free distribution (IFD), they will divide themselves among the habitats in such a way that the fitness returns per individual in the better habitat (with  $d_2$  competitors) are the same as in the worse habitat (with only  $d_1$  competitors). In this way, no animal could increase its fitness by moving to the other habitat (check it out for yourself). For this solution to be correct, several assumptions have to be true (see Milinski 1979, Milinski et al. 1995). First, individuals are free to leave or enter a patch. There is no aggressive defense of patches. Second, each individual chooses the most profitable patch available at a given moment. This assumption implies perfect knowledge of the gain rates in different patches. Third, all individuals have the same expected intake [fitness

gain] rates within each patch. This last condition thus implies effectively equal competitors, which can be true in some conditions, but is not generally true.

In an extension of ideal-free theory, it has been shown that the IFD will occur even if individuals differ in fitness gain rate **IF AND ONLY IF** the relative gain rates of different, unequal individuals do not differ between patches. So, if the less successful types do half as well as the better ones in patch A, they must likewise do half as well in patch B, patch C, etc. This condition might often be true if the differences in gain rate are due to factors other than aggressive competition, such as age, sex, experience, or nesting status. However, if differences in success are due mostly to differences in fighting ability, and thus the ability to defend favored sites, then the relative success of different types will depend on the density of individuals and the distribution of the resources being contested. If the resources are clumped, this usually favors aggressive defense and increases the relative fitness gain of aggressively successful animals ('bullies') relative to less successful ones ('wimps'). When resources are widely spaced or sparse, then bullies and wimps can often do equally well, or at least the differences in fitness gains are much reduced. Thus, when resources differ in spatial arrangement, we might **NOT** expect the ideal-free distribution to occur. Note that this might also occur simply because individuals are not free to enter or leave patches (but this is equivalent to saying that the excluded individuals have zero fitness gain from the patch that they cannot enter).

What do we expect to happen when aggressive competition produces different **RELATIVE** fitness gain rates for distinct classes of individuals across patch types? Deriving the answer is complicated, but the answer is fairly simple: each class of individuals will prefer a patch type (or range of similar patch types) where their **RELATIVE** feeding rates are greatest compared to other classes of individuals. Such phenotype-dependent distributions among patch types are generally called truncated phenotype distributions or TPD. In theory, these preferences are non-overlapping or just barely overlapping (any one patch type would host at most two classes of individuals), leading to what is called a 'perfectly truncated phenotype distribution'. An example is given below:



In practice, for many reasons, such nearly complete segregation of feeding classes is not really expected. Rather, we expect to see 'partially' truncated phenotype distributions, in which better competitors prefer better patches, but some wimps may occur there as well. In any case, the differences in feeding success should **NOT** be zero **BETWEEN** classes of competitors, but **SHOULD** be (close to) zero among individuals **WITHIN** a class.

## Feeding the wildfowl: the natural history

The purpose of today's lab is to apply and test the concepts of ideal-free distributions and truncated phenotype distributions to the spatial choices of birds competing for bread cubes at the Stony Brook Mill Pond. These birds are used to being fed by humans, and often more than one family feeds them at the same time, so they must make choices about where to feed. We will offer the birds one or more feeding spots with different rates and spatial arrangements of food rewards, roughly following the experiments described in Milinski et al. (1995). Like that paper, we will need to deal with several different types of birds feeding: swans, Canada geese, ducks, and gulls. These are arranged in order of decreasing size and competitive ability in the water, although the gulls often try to preempt the bread cubes by catching them in the air. Unlike Milinski et al., we will not attempt in this lab to generate a random distribution of bread cubes, nor measure a strictly defined area with a camera. These are desirable touches but require too much equipment and setup time for us now (however, they might be possible for students who wish to pursue this as an independent project). We will discuss ways in which we might design the experiment to get around these technical problems. Think about the following questions:

- 1) Given the different aggressive abilities (mostly due to body size) of the different bird species, how can we design a test of the IFD? What ways of feeding are most likely to neutralize the RELATIVE advantages of the larger, more aggressive species?
- 2) What 'mistakes' did Milinski et al. (1995) make in their experiment? Why were their two patch types not sufficient to test the TPD? How many patch types do you think we should set up, if time and personnel were not limits? What natural history factors that they could measure might have led to a partial TPD? (Hint: they mention one 'exceptional' subadult swan).
- 3) Why is it important that the birds be able to sample all patch types? How could you test the importance of such sampling to the generation of an IFD or TPD? (Hint: what factors would discourage sampling? How can you measure the impact of sampling?)
- 4) If bullies simply exclude wimps from good patches (i.e., wimps are not free to enter patches), how should this affect the predictions of TPD?
- 5) How is the overall composition of the bird 'community' likely to affect our experiment? Contrast in your mind a pond with almost all ducks and a few swans against one with mostly swans and a few ducks.