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Altruism is often referred to as an evolutionary mystery because evolution makes organisms maximize fitness, while under altruistic behavior organisms sacrifice their own fitness for the good of the group. The way out of this is to observe that evolution operates on genes, not individuals, and that *altruism works as long as its benefits are enjoyed primarily by other altruists*. Three mechanisms are commonly studied:

- (a) Kin selection is often phrased in the terms of Hamilton's rule, altruism is favored $rB > C$, where r is the relatedness, B the benefit received and C the cost to the altruist. The primary example of kin selection is haplodiploidy in hymenoptereans, (bees, ants, etc). Males are haploid while females are diploid, hence offspring from the same queen (siblings) are on average $3/4$ related to each-other, while if a worker is only $1/2$ related to its own offspring. Consequently the worker should sacrifice its own fitness to help the fitness of its queen mother. This idea has been challenged on the basis of the observation that many times the queen has been multiply mated, so the relatedness argument breaks down. If this were the case, altruistic behavior of eusocial insects could instead be explained by group selection, (argument following). However, a study in Science earlier this month demonstrated that the ancestral state of all multiple-mating species is a monogamous one, and also showed that in cases where the queen is multiply mated, the workers are less totipotent, unable to have offspring.
- (b) Group selection works by any system which allows altruists mostly to benefit other altruists. A good thought-experiment example is the

following. Imagine a population that spends most of the year in small groups, but then comes together to breed and die. Offspring then randomly assort into small groups again. The small groups with mostly altruists come back fat and happy each year, even if a cheater among them has also benefited, he is only one out of a group that is mostly altruists. Being fat and happy, they have many offspring. A group with mostly cheaters straggles in, lean and flea-ridden. They manage to have few offspring. Consequently, altruists represent a disproportionate share of the parents of the next generation, and altruism spreads. This can be made into a precise statement about covariances, but is clearly seen to work in this simple example.

- (c) Reciprocal altruism is the idea that I'll do something good for you today (i.e. share my food with you if you didn't get any – like vampire bats do) if you reciprocate tomorrow when I don't get any food. Trouble is, the obvious incentive is not to reciprocate, take but not give. Cheaters can be caught by policing if it is possible to identify individuals.

1 2b

Optimal foragers decide whether to specialize on 1 resource if (according to the theory of MacArthur & Pianka):

$$\frac{E_2}{h_2} < \frac{\lambda_1 E_1}{1 + \lambda_1 h_1} \quad (1)$$

where λ_1 is the encounter rate with resource, E_i the energy content of a unit of resource i , and h_i the handling time of resource i . The optimal forager must know all these values. (Actually, it will suffice for instance for the optimal forager to know only the ratio E_2/h_2 , and not the individual values, but that's not important). A key observation is that the encounter rate of the inferior resource λ_2 (inferior in the sense $E_2/h_2 < E_1/h_1$) does not matter.

A forager can cope with uncertainty in a variety of ways. First we describe coping with uncertainty in the parameters of the MacArthur and Pianka model using bet hedging. Then we will address more general concerns about uncertainty that are not incorporated into the model, which depends on state. One form of uncertainty would be in the payoff, E , of a resource type. We could imagine one resource with the potential for very high payoff if attacked

(say, fitness of 4), but also could have a very low (or negative) payoff (say, with probability $1/2$ of getting fitness benefit $1/8$) if the attack plan goes poorly (think lion vs bison). We consider a second resource with a predictable but poor payoff (lion eating mice), possibly not even enough to save energy for offspring (say, fitness benefit of $4/5$). By bet hedging, hunting both resources in the optimal frequency, the lion can gain energy even if specializing on either one type would cause him to get no fitness. (Simply calculate the mean log fitness of the options provided). This results in generalizing being optimal, even though using the average E_1 in equation (1) can tell you to specialize.

Foragers method of dealing with uncertainty (risk) often depends on their state, even though state dependence is ignored in the original model. The principle of asset protection says that foragers who have a good state should be risk adverse, while foragers with a low state should be risk prone, particularly when facing a time horizon, such as a breeding period. This is a simple application of Jensen's inequality: individuals should be risk prone when the per fitness benefit has positive second derivative, and risk adverse if the fitness benefit has negative second derivative, see Figure 1. Experiments have determined many organisms are risk adverse, which suggests that they are using a diminishing returns risk function.

Many other methods exist to deal with different kinds of uncertainty. Some involve reducing the uncertainty by sampling the environment, as opposed to the methods like bet-hedging described here that simply deal with the uncertainty. Sampling methods come at some cost, resulting in another optimization problem.

3b

Plastic responses can be a valuable way for a population to deal with uncertainty. Plastic developmental morphology might allow a creature to be better adapted to its environment than a fixed morphology, for instance, if larval forms experience extensive dispersal across a variety of environments. For instance, we might consider a marine invertebrate whose developmental pattern will be a plastic response to whether it lands on rock or on sand, where it switches to the morphology better designed to attach itself to such a substrate. However, plastic developmental responses will have some error rate, where occasionally the wrong morphology is chosen for that environment. In this case the individual will probably do worse than a non-plastic

counterpart with a morphology equally adapted to each environment but optimized for neither. Traditional theory aims at predicting how to balance the benefits of the plastic matching the environment with the cost of mismatching. However, an individual that is also capable of a fast plastic response, such as a change in behavior (or equally important, a reversible response), may be able to offset the cost of mismatching by a change in behavior. Consequently, in a scenario where morphological plasticity may be maladaptive (cost of miss-matching outweighs the benefit), allowing a plastic behavioral response may make the morphological plasticity adaptive again. If the benefit of the behavioral plasticity helps primarily when the creature is badly mismatched, but offers less benefit to a creature who is equally adapted to each environment (i.e. the behavioral benefit shows diminishing returns with better matching), then this could create a plasticity syndrome, where behavioral plasticity would couple to morphological plasticity. However, if the benefit showed a convex response to mismatching, where the benefit of the behavioral plastic response was greater the more matched the morphology, then we'd expect the morphologically unplastic one to show more behavioral plasticity instead.