

## PRUDENT PREDATION AND THE CHARACTER OF ECOLOGICAL ATTRACTOR SETS

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Many human observers have judged some or all predators to be prudent. That is, the human observer feels that the predators could harvest more prey simply by making some minor modification in their behavior, morphology or physiology that seems to be easily within their evolutionary grasp. For example, the predator might sleep less, digest more of the prey, hunt in teams, run faster, crowd together more tightly on smaller territories, or reproduce at a higher rate.

Some people who have thought deeply about predator-prey systems (e.g., Rosenzweig [8]) conclude that the predators are, in fact, as efficient as evolution permits. It is not that some static limit is reached, for the predators do evolve better tactics and bodily apparatus. But the prey counter this with compensatory evolution on their own part. Such evolution evokes thoughts of the Red Queen who told Lewis Carroll's young heroine that she had to run very fast simply to stay where she was and even faster to get somewhere (Van Valen [11]). Schaffer and Rosenzweig [9] believe that the predator and prey rates of evolution exactly cancel and that the system dynamics are likely to remain constant over long stretches of evolutionary time. Such a view, however, borders on orthogenesis. Most evolutionists with a good grounding in genetics view evolution as a halting process, a process with different gaits. Yet, if such temporal irregularities are minor, the argument of Schaffer and Rosenzweig retains its force. But if it is occasionally the case that predators could or do evolve something for which the prey have no answer, then another explanation for the prevalence of prudent predators is required.

Some scientists believe that predator individuals are indeed prudent, and that they are themselves responsible for this fact. They believe this to be the result of the normal sort of Darwinian evolution. The selfish genes of each predator individual are doing the best they can. If such a predator did take more prey, he would indirectly harm other predator individuals around him, and these individuals might be his kin; that is, they will likely share many of the same genes. In such a situation, any gene for imprudence will hurt other copies of itself. Thus on the evolutionary balance sheet this genetically based trait might prove unprofitable. Such kin selection is particularly likely to occur when a popu-

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lation has the kind of breeding structure described by D. S. Wilson [12], in which during one stage of the life cycle the individuals of the population are distributed into "trait groups." If there are two genetic types—prudent and imprudent—they should at least be distributed in a binomial fashion, which causes each individual to experience a disproportionately large number of interactions from its own type. And mechanisms exist, e.g., positive assortment and multiple oviposition, to make the distribution even greater than binomial, thus magnifying the effect. A trait group of imprudent predators might do considerable harm to one another, making the total output from the patch low.

The problem is that most predator species do not have the breeding structure that will support the above analysis. An animal's neighbors, i.e., those that would be most directly harmed by its imprudent behavior, are normally not close kin and are no more likely to share genes than any two animals picked at random. Thus, the predator has no evolutionary brakes on the evolution of its greater efficiency. Predators should not be prudent. If they are, the explanation must lie elsewhere.

Group selection is a possible answer. Before considering how this works it is important to comment on the unfortunate character of the name. "Group selection" suggests that the basic evolutionary unit is no longer the individual and his selfish genes. Group selection was first conceived by Carr-Saunders [1] as applying to human cultural groups. Such groups have an evolutionary integrity beyond the individuals which comprise them. They can compete one against the other and can remain unchanged even after absorbing the individuals of another group.

This form of group selection was applied by Wynne-Edwards [13] in rather uncritical fashion to explain prudence in animal populations. But prudence, if it exists in animals, cannot be based on culture; it must be the result of genetically controlled behaviors. Wynne-Edwards did not supply a genetic model. And even though he probably had most of the essentials for such a genetic model, his ideas came under heavy attack.

The first genetical model of group selection was produced by Levins [5]. In his model the extinction probability of a predator group was dependent on the frequency of a gene; he assumed that it would be linearly proportional to the frequency of this gene. Individual selection was assumed to favor increases in the same gene frequency. In the metapopulation (i.e., a region containing many environmental patches on which groups can exist), groups that go extinct are recolonized from extant groups; random founder effects play a role in setting the new frequency. Over a metapopulation of such groups, which way will the gene frequency move? Will the group extinctions, i.e., the group selec-

tion, override the individual selection and drive the gene frequency lower? Levins thought not. Gilpin [2], working with an idea conceived independently by MacArthur [6] and May [7], extended Levins' model by making the group extinctions depend explicitly on predator over-exploitation of the prey. He was much more sanguine about the possibility of group selection.

These genetically based models of group selection do not depend on direct interaction or competition between groups. Rather, they depend on the avoidance of group extinction caused from internal causes, i.e., the overexploitation of prey. Groups that, by the normal stochastic processes that impinge on gene frequencies, keep a low frequency of genes for high exploitation efficiency will survive longer than other groups and will likely be those that serve as the pool whence individuals recolonize ecological islands on which other groups have gone extinct.

Gilpin's analysis showed that genes for prudence are most likely to win out when group extinction occurs quite suddenly upon the attainment of a low threshold frequency of the imprudent type. The two allelic genes in his model controlled one or another parameter for exploitation efficiency. This parameter changed smoothly with gene frequency. The extinction threshold corresponds to the point where the parameter change causes a Hopf bifurcation away from steady-state to a limit cycle. The amplitude of the limit cycle increases very rapidly with changes of the parameter. With a small percentage increase of the parameter, the limit cycle is crowded up against one or the other of the axes which, for a biological system, spells extinction of the predator in either case. Within the contest of a one predator and one prey system, the model was shown to be robust.

Recently the behavior of some multispecies systems under parameter changes that correspond to increased predator exploitation efficiency was investigated by the author. In one system, the prey was modeled implicitly. Three predators interacted by means of their carrying capacities on this resource dimension. Increases of one carrying capacity could cause the system to go into the kind of limit cycle oscillations described by Gilpin [3]. In such a case, one of the predators will randomly go extinct, after which competitive exclusion will proceed against one of the remaining two predators. Thus, the predator that does evolve the increased exploitation efficiency will have a 2/3rds probability of going extinct because of it. This is something with very serious evolutionary implications and is probably sufficient to make for group selection and the maintenance of prudence.

In a second model, the dynamics of a two prey and one predator system (Gilpin [4] and Vance [10]) was studied. This system behaves much

the same way as a one prey and one predator system. But one difference is that bifurcations to attractor sets other than limit cycles are possible. In this case the attractor set is spiral chaos. But it has the same property of reaching extremely low predator densities with small increases of the predator exploitation efficiency. Again, group selection for prudence is likely.

These studies lead to the following conjecture: For ecological models of form

$$\dot{N}_i = N_i f_i(N_1, N_2, \dots, N_m), \quad i = 1, 2, \dots, m,$$

where each species  $i$  is self-limited ( $f_i(N_1, N_2, \dots, N_i, \dots, N_m) < 0$  for  $N_i > L_i$ ), the attractor sets are either stable steady states or attractor sets that approach to less than one individual of at least one axis; the volume of parameter space corresponding to transition between stable steady states and these attractor sets will have a relative volume approaching zero.

If this conjecture is true, the implication will be that group selection will occur whenever systems are destabilized from steady state. Thus all predators will be limited in their exploitation efficiency and thus prudent.

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