

## EVOLUTION AS A ZERO-SUM GAME FOR ENERGY

Leigh M. Van Valen  
 Department of Biology and  
 Committee on the Conceptual Foundations of Science  
 University of Chicago  
 915 East 57th Street  
 Chicago, Illinois 60637  
 USA

Received September 21, 1978

**ABSTRACT:** Energy controls evolution, and for any evolutionary unit at any time scale natural selection maximizes the expected amount of energy available for (approximately) growth and reproduction. The amount of energy available to any set of mutually interacting organisms is roughly constant, so a zero-sum competition results. Natural selection occurs at all time scales simultaneously. This leads to predominantly maximean strategies on shorter time scales and maximin strategies on longer ones. All organisms play against all other organisms with which they interact. Ordinarily the physical environment merely sets the conditions of the game. Coalitions occur, though not in general optimal ones, but spatial variation can often give results like rational communication among species. There is never a final payoff, and new competitors replace the losers. Game theory itself needs modification to apply to evolution.

\*

\*

\*

Energy controls evolution just as it controls other natural processes. Yet the amount of available energy (more strictly, the amount of power) is limited. Each organism strives to obtain as much of this energy as it can. There is therefore conflict, premature death, extinction, differential expansion, and, as both a mechanism and a consequence, evolution. In this short paper I can only summarize the biology as I see it and indicate its pertinence to game theory. My closest predecessors, in one way or another, are Charles Darwin (1859, 1975), Alfred Lotka (1922, 1940), Bertrand Russell (1927), Ronald Fisher (1930), Raymond Lindeman (1942), Evelyn Hutchinson (1948), and George Simpson (1949). Perhaps Howard Odum (1971) should be included, but I have found his work incomprehensible. My general approach has been justified and presented in more detail by Van Valen (1973, 1974a,b, 1975a,b, 1976a, b) Maynard Smith (1976a,b), and Zuckerkandl (1976). The section on biology is partly extracted from previous papers.

## BIOLOGY

Consider a forest, rich in species of plants, animals, fungi, and the lesser beasts of the interstices:

Sunlight comes to the forest bearing energy. Some is reflected, some is absorbed by non-photosynthetic tissues as heat, and some is used to reduce carbon from CO<sub>2</sub> and hydrogen from H<sub>2</sub>O. The part that is so used can be used only once: what one plant uses, absorbs, or reflects away is unavailable to any other plant. Most of the sunlight is taken care of in these ways, so the floor of a mature forest is relatively dark as compared to the light above the canopy. Water or other nutrients (or space) are sometimes regulatory, but this merely blurs the edges of the picture because they too will then be competed for. For any ultimately regulatory resource, what one species or individual gains, the rest lose. This is the central point.

\*

\*

\*

\*

\*

\*

\*

The point applies to animals too, even more strongly. The plants reduce a certain amount of carbon each year. Much less than 1 percent of this net amount is ultimately lost to sediments; all the rest is oxidized by animals, fungi, and microorganisms (and also, on land, by fires). Each reduced carbon atom is fully oxidized only once. For heterotrophs as for green plants, what one gains, the rest lose.

This is the Red Queen's Hypothesis: A change in the realized absolute fitness of one species is balanced by an equal and opposite net change in the realized absolute fitness of all interacting species considered together. By the realized absolute fitness of an individual or taxon I mean, approximately, its control of trophic energy.

Potential energy in the form of reduced carbon is the fuel of the fire of life. All other resources, even when regulatory, can be considered surrogate resources when they are competed for. Competition for them is effective only to the extent that it permits greater control of the trophic energy. Competition for surrogate resources involves strategies to get more energy.

Several things are essential to our form of life: energy, space, various elements, suitable temperatures, etc. But trophic energy is paramount in biological processes at all levels for the same reason that energy is paramount in physics, in geology, in chemistry: it is causal; it drives the dynamics.

Now consider the ABO blood group in Homo sapiens. Thompson (1972) has shown that, if current trends continue, the alleles for group A will decrease in frequency from 0.215 to 0.205 in this species in about the next 35 years. This is a directional evolutionary change. It is nonrandom. It is somehow selective. It is extraordinarily rapid. However, it is caused entirely by different growth rates of different populations. These populations differ in their ABO frequencies, and A alleles are relatively uncommon in most groups that have both large size and a high rate of increase. The evolutionary change is not caused by properties of individuals or of the blood groups themselves, and there is no extinction or founding of groups. The process therefore doesn't fit existing categories of selection, and Thompson in fact considered it nonselective. However, it also doesn't fit any other recognized evolutionary mechanism, and I think it is apparent that the evolution is occurring because some groups are more fit than others, as a result of group properties (culture). The process is therefore selective.

Thus we see here in pure form a commonly unrecognized component of selection and of fitness; it may be called expansion. Most evolutionary change now in the composition of Homo sapiens is caused not by individual selection or by turnover of new and old groups, but by differential growth rates of persisting and diffusely founded populations, and these rates themselves are caused by group-level properties. Some groups (and their genotypes) come to control more trophic energy than before even when there is no change of the composition within groups and no extinctions or new groups.

Expansion is the only component of fitness involved. It may be defined as an increase or decrease (negative expansion) in the size of single evolutionary units as they persist. And size is best measured by trophic energy control. The energy available for growth and reproduction can be called expansive energy. Expansive energy is a better approximation to total fitness (on which see below and Van Valen, 1976b), than is all trophic energy controlled, and it is adequate for most purposes. Defining fitness by means of numbers of offspring or other individuals, as is usually done for historical reasons, has serious disadvantages (Van Valen, 1976b).

Natural selection is the action of fitness in causing differential expansion of evolutionary units, which may intergrade with each other. We recall that realized fitness is expansive energy in some real environment. It is then easy to show that natural selection on any evolutionary unit at any single time scale, maximizes the expected amount of expansive energy for that unit at that time scale. The domain of this law is less than universal, and of course the maximization is local rather than

global because of the hill-climbing mechanism. Natural selection acts on each unit of evolution so that as much as possible of the trophic energy in the environment is turned into expansive energy of that unit. All else in biology is mechanism to that goal. As Bertrand Russell (1927, p.27) put it, "Every living thing is a sort of imperialist, seeking to transform as much as possible of its environment into itself and its seed." To a naive observer, untroubled with existing theories, it is one of the most striking aspects of the living world.

Natural selection maximizes many quantities if all else is equal in each case, but only expansive energy is maximized unconditionally. The use of energy makes all forms of natural selection commensurable and permits unified analysis at all levels.

Available trophic energy does not increase or decrease indefinitely at any evolutionarily important rate. This is a major part of the ancient idea of the balance of nature. There is even suggestive geochemical evidence (Van Valen, 1976b) that the worldwide level of photosynthesis has been constant at geochemical accuracy for  $10^9$  years or more, i.e. constant within an order of magnitude with the possibility of brief excursions of greater amplitude. Such a degree of constancy is much greater than is necessary for the operation of the Red Queen at ordinary evolutionary time scales.

The domain of the Red Queen is not universal and its boundaries are hard to survey even approximately. On a short time scale, primary productivity often changes during ordinary community succession, although the change is rather small and the area of interest should perhaps usually be a region large enough to contain a steady state of such local successions. Only in such a region would fugitive species (Hutchinson, 1951) persist. Fluctuations in weather, nutrients, and the like also affect productivity. To some extent the Red Queen is immune to such perturbations, but how far such robustness extends, and under just what conditions, is still unclear. There is evidence that great crises such as those at the end of the Paleozoic and Mesozoic do impinge on the Red Queen's domain seriously although briefly. The occupation of habitats for the first time by organisms also falls outside the domain. This is true not only for new types of habitat, as in the initial invasion of the land, but also for new lakes or islands or rock surfaces when we are using a time scale too short to invoke a steady state of origin and disappearance of such habitats.

Evolution proceeds simultaneously on all time scales from an hour (some bacterial competition) to  $10^8$  years or more (competition of some higher taxa). There is no natural time unit for evolution. Geneticists often use generation length as a standard, but ecologists know that organisms with different generation lengths interact, even within populations of one species. And time scales are fundamental in evolution. The difference between most kinds of individual and group selection can be viewed alternatively as a difference in time scale. This can be seen best by an example. Self-regulation of population density is disadvantageous at the individual level but advantageous at the group level, and is Wynne-Edwards' prime case (1962) for group selection despite doubts that it exists. However, it is advantageous to individual phenotypes and genes on a long time scale. How one views the process is then a matter of taste. As with dispersal away from a population (Van Valen, 1971a) and other group-selected features, the time scale can be interchanged with the level of selection.

Phenotypes are what natural selection acts on, yet geneticists such as Lewontin (1974) think they are unimportant evolutionarily because they disappear each generation as the individual dies. This is a strange view to a paleontologist. Phenotypes recur in other individuals and so natural selection has its chance again. Because the phenotype changes with age and selection acts at all ages, it is useful to think of evolution as the control of development by ecology. Curiously, neither development nor ecology, i.e. neither of the two central areas, has had much of a role in evolutionary theory since Darwin. It is the ultimate regulatory factors of its population density which determine whether a phenotype can persist in a community. This is just as true at the species level as at others and suggests that species should be looked at primarily from an ecological rather than a genetical viewpoint (Van Valen, 1976c).

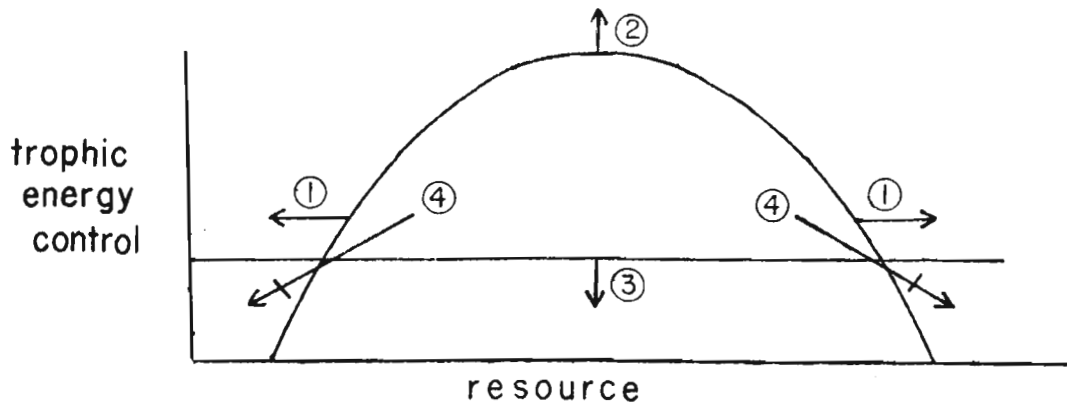


Figure 1. The four ways in which a population can increase its effective trophic energy. 1: extension of the favorable region of the adaptive space (limiting factors.) 2: Increase of total energy control (regulatory factors.) 3: Lowering of line of expansive sufficiency (direct factors.) 4: Reduction in energetic subsidy of unfavorable regions of the adaptive space. ns: line of adaptive sufficiency.

\*\*\*\*\*

A population can increase its useful expansive energy in exactly four ways (Figure 1). One is by enlarging its favorable region, the part of the adaptive space where it gains enough energy for growth and reproduction. This involves selection to overcome the limiting factors of its ecological or geographic distribution. The second way is by increasing its total energy control. This involves selection to overcome the factors that ultimately regulate its density. Thirdly, it can lower its line of expansive sufficiency, the upper boundary of the energy wasted and used for maintenance in different parts of the adaptive space. This is done by selection on (other) direct, and mostly on dominant, factors, and need not always be in the favorable region. Finally, a population can reduce its energetic subsidy of the unfavorable regions of the adaptive space. Because this reduces the population's force of expansion and therefore its effectiveness in competition, this mechanism is probably uncommon except in directions where there are no competitors. These four processes seem to partition natural selection exhaustively.

Fitness is the central concept of the evolutionary half of biology, yet it is an exceedingly elusive concept. In population genetics it is the number of offspring, usually one generation later, and this notion is usually adequate within the domain of genetics. But when the domain is expanded the inadequacy of considering only numbers of individuals becomes apparent. Individuals differ in their size and other aspects of quality, and even the boundaries of an individual are arbitrary in many kinds of organisms. The means of control of the numbers of individuals in a population is ignored, yet this can strongly interact with their quality. And so on. In any real case natural selection has a single and well-defined outcome, so the problem is in our analysis rather than in the real world. Energy provides the unifying mechanism. In the usual domain of population genetics it reduces to the standard concept, as it should, but it permits a single analysis at all levels. It permits such a single analysis because it drives all processes and is the single ultimate currency.

#### GAME-THEORETICAL ASPECTS

Because the Red Queen sees the amount of available trophic energy as constant to a useful approximation, she views evolution, and ecology in general, as a zero-sum game. Ecology is broader than evolution here because the best strategy may be not to evolve.

Who are the players? Since Lewontin's seminal paper (1961) it has been customary to think of organisms playing nature. The Red Queen sees organisms playing each other. Any game or conflict occurs in some context, which includes the rules but is not always restricted to them. In chess any context beyond the rules may be ignored; in politics it cannot be. Perhaps it cannot be ignored in any conflict that is not artificially isolated. Nature is the context in which the game of evolution takes place. Player A may be better in one part of the environmental or contextual hyper-space, player B in another; strategy  $\alpha$  better in one, strategy  $\beta$  in another.

The spatiotemporal structure of the environment is therefore of major importance in competition in the real world.

The players are whatever units of evolution one is considering: alleles, phenotypes, species, clades, or others. In the real world they all play at once, at different levels or time scales. The environment determines the nature of the game and is itself predictable to an extent which depends on the situation and time scale. Predators compete with decomposers and herbivores for the energy fixed by green plants, and herbivores compete with the plants themselves as well as with members of their own trophic level.

How many players are there? All species in a community degrade the available energy. There are as many players as there are units of evolution at a given level. Single interactions can be abstracted from the whole for ease of study, but it is futile to try to build a general theory from such artificially isolated bits. Evolution is ordinarily irreducible to a two-person game. The number of players changes; new species or alleles appear *de novo* or by immigration, and old ones become extinct at least within one's domain of interest. And the domain itself usually has very fuzzy boundaries, a matter which has been the particular preserve of phytosociological botanists.

What strategy should a unit of evolution follow? As we will see, this is not necessarily the same sort of strategy that it is able to follow. Lewontin (1961) and others have advocated a maximin metastrategy, the avoidance of extinction. But this is only part of the picture. It is roughly the part left when expansion is ignored, and expansion was only recently recognized as a component of fitness in its own right. Short-term strategies are usually *maximean* strategies, maximizing the expected fitness on the given time scale. For fugitive species and the like this may involve local extinctions as a way of life. Short-term evolution maximizes the expected expansive energy within a group rather closely, but in long-term evolution extinction is more important than short-term maximization.

The maximin metastrategy involves buffering against the effects of environmental shocks; this is why such buffering is occasionally equated with fitness (e.g. Lewontin, 1958). It can operate at the individual level, as by homeostasis or resistance to predation; at the population level, as by density-dependence or cooperative behavior; or at higher levels, as with fugitive species. As the examples indicate, some adaptations serve both maximin and maximean metastrategies. But the strategies for different time scales often conflict with one another; one time scale may predominate or the balance may shift. Strategies close to the maximin extreme, where bare survival is all-important, are developed on the time-scale of extinction even though they are continually eroded and even eliminated by short-term development of adaptations that give a maximean strategy before extinction. Thus strategies themselves compete (Van Valen and Maiorana, MS) although, depending on their mutual compatibility (cf. Levins, 1962), the result may be a compromise rather than a polymorphism or exclusion.

There is nothing paradoxical about natural selection acting in opposite directions on different time-scales. But to the extent that our basic idea of fitness is whatever natural selection maximizes, the existence of more or less independent processes of natural selection on different levels and different time-scales totally precludes any concept of fitness that is both general and precise. This is the well-known conflict of adaptedness and adaptability explicitly treated as a continuum. To quantify the nature of the imprecision, a general definition of the fitness  $F$  of any biological unit may be expressed as

$$F = \int_0^{\infty} w(t)e(t)dt,$$

where  $e(t)$  is the expected value, relative to information available now to the organism or to an observer, of the amount of expansive energy of the unit at each time  $t$  in the future, and  $w(t)$  is an arbitrary weighting function, the same for all units in

any one comparison, for which I would choose an exponential decline at a low rate. Fitness is of course game-theoretic utility in the game of evolution. But evolution consists of many games, at different time-scales, played simultaneously, and criteria of fitness in these different games commonly conflict.

No unit of evolution chooses a strategy. Such strategies are themselves selected for, at each time scale, and are of prospective use only as a byproduct of the past. How useful they prove to be depends on the predictability of relevant environmental patterns. And the strategies themselves are continually modified: evolutionarily stable strategies (Maynard Smith and Price, 1973) may be only temporarily stable. We can usefully speak of strategies at all only because of the teleological (in Aristotle's sense, not that of mystics implying purpose) nature of organisms. This teleological nature itself exists only because of three things: natural selection, the repetition of life cycles and their phenotypes, and a degree of environmental predictability. Strategies of opponents are known in the same way as are other aspects of environmental predictability, by learning or by natural selection, the close evolutionary analog of learning.

An optimal strategy may not be adopted; the path to it may be blocked or too hard to find. Perhaps development cannot be modified directly in that way, perhaps appropriate allelic combinations fail to occur often enough to be selected (if at all), perhaps a poorer strategy must intervene before the best one appears (local maxima may not be global), or perhaps a strategy on one time-scale precludes optimization at another.

It is sometimes useful to consider strategies against the physical environment. Usually this is an aspect of competition with other evolutionary units for energy, but in extreme habitats it can be a matter of simple survival. In such a case there is no zero-sum constraint, but the goal is still maximization of expansive energy.

A zero-sum constraint is a strong one and unfortunately is not always applicable. It is a realistic idealization: exceptions are important in only some ways. Second-order modifications of the constraint must be permitted but the first-order situation deserves first attention.

As Simon (1962) and others have noted, complexity often brings its own regularities and simplifications. We need not study major patterns of evolution by building from pairwise interactions. But such interactions are sometimes instructive. Cooperation occurs among some organisms as a mechanism of more effective competition with others. Such coalitions are well known in human competition. When rational communication is impossible, however, optimal strategies may also be impossible. This prisoner's dilemma happens in evolution too. Two species can easily evolve interference mechanisms against each other with the result that neither gets as much energy as it would without the interference (Van Valen, 1976b). Perhaps some other species uses part of that energy, or perhaps the interference itself uses it all. However, spatial variation can take the place of rational communication in many cases (Wilson, 1976). Patches with the best cooperation can expand to replace those depleted by internal competition. Such a resolution of the prisoner's dilemma may have application outside ecology.

When does the payoff occur? It never does, in a final way. A unit of evolution can completely lose but it can never completely win. On the other hand, provisional payoffs must occur continually (sporadically if one is considering very short-term time scales) so that the players can survive. All players must use energy for maintenance, but this can usually be ignored on an evolutionary time scale. Some players fail to survive, but on the average others take their places.

A modified game theory would thus seem to be one of the more promising ways to approach evolution. To a good approximation, each species or other unit is part of a zero-sum game against other species. Which adversary is most important for a species may vary from time to time, and for some or even most species no one adversary may ever be paramount. Furthermore, no species can ever win, and new

adversaries grinningly replace the losers. This game is rather different from those normally analyzed, but we must not modify the biology to fit available theory. An extension of theory to accommodate such a game could have valuable and unforeseen results.

\* \* \* \* \*

## LITERATURE CITED

- Darwin, C. 1958. *On the Origin of Species by Means of Natural Selection*. London: J. Murray. 502 pp.
- \_\_\_\_\_. 1975 *Charles Darwin's Natural Selection*. Cambridge: Cambridge University Press. 692 pp.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press. 272 pp.
- Hutchinson, G. E. 1948. Circular causal systems in ecology. *New York Academy of Science, Annals*, 50:221-246.
- \_\_\_\_\_. 1951. Copepodology for the ornithologist. *Ecology*, 32:571-577.
- Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *American Naturalist* 96:361-373.
- Lewontin, R. C. 1958. The adaptations of populations to varying environments. *Cold Spring Harbor Symposia on Quantitative Biology*, 22(for 1957):395-408.
- \_\_\_\_\_. 1961. Evolution and the theory of games. *Journal of Theoretical Biology*, 1:382-403.
- \_\_\_\_\_. 1974. *The Genetic Basis of Evolutionary Change*. New York: Columbia University Press. 346 pp.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.
- Lotka, A. J. 1922. Contribution to the energetics of evolution. *Proceedings of the National Academy of Sciences (U.S.A.)*, 8:147-154.
- \_\_\_\_\_. 1940. The place of the intrinsic rate of natural increase in population analysis. *Proceedings of the 8th American Science Congress*, 8:297-313.
- Maynard Smith, J. 1976a. A comment on the Red Queen. *American Naturalist*, 110: 325-330.
- \_\_\_\_\_. 1976b. What determines the rate of evolution? *American Naturalist*, 110: 331-338.
- \_\_\_\_\_. and G. R. Price. 1973. The logic of animal conflict. *Nature*, 246: 15-18.
- Odum, H. T. 1971. *Environment, Power, and Society*. New York: J. Wiley. 331 pp.
- Russell, B. 1927. *An Outline of Philosophy*. London: G. Allen and Unwin. 307 pp.
- Simon, H. 1962. The architecture of complexity. *American Philosophical Society, Proceedings*, 106:467-482.
- Simpson, G. G. 1949. *The Meaning of Evolution*. New Haven: Yale University Press. 364 pp.
- Thompson, E. 1972. Rates of change of world ABO blood-group frequencies. *Annals of Human Genetics*, 35:357-361.
- Van Valen, L. 1971. Group selection and the evolution of dispersal. *Evolution*, 25:591-598.
- \_\_\_\_\_. 1973. A new evolutionary law. *Evolutionary Theory*, 1:31-49.
- \_\_\_\_\_. 1974a. Molecular evolution as predicted by natural selection *Journal of Molecular Evolution*, 3:89-101.
- \_\_\_\_\_. 1975a. Group selection, sex, and fossils. *Evolution*, 29:87-94.
- \_\_\_\_\_. 1975b. Reply to Foin, Valentine, and Ayala. *Nature*, 257:515-516.
- \_\_\_\_\_. 1976a. The Red Queen lives. *Nature*, 260:575.
- \_\_\_\_\_. 1976b. Energy and evolution. *Evolutionary Theory*, 1:179-229.
- \_\_\_\_\_. 1976c. Ecological species, multispecies, and oaks. *Taxon*, 25:233-239.
- Wilson, D. S. 1976. Evolution on the level of communities. *Science*, 192:1358-1360.
- Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behaviour*. Edinburgh: Oliver and Boyd. 653 pp.

Zuckerkindl, E. 1976. Evolutionary processes and evolutionary noise at the molecular level. II. A selectionist model for random fixations in proteins. *Journal of Molecular Evolution*, 7:269-311.

## OPEN DISCUSSION

William Wimsatt, University of Chicago: Have you given any more thought to the relationship between your account and Simon's satisficing or other heuristics?

Van Valen: The hill-climbing mechanism that I use here is more general than satisficing. It can be partitioned into two aspects. One is ordinary maximization, where one actually gets to the top of the hill. The other hand is satisficing, where one gets gigh enough and that's good enough. That is, the difference between these two depends on the presence or absence of a threshold, which may be fuzzy, and if one gets past the threshold that's good enough. Everything above the threshold may be selectively equivalent. I'm not sure that this is particularly useful in an evolutionary context because fitness is always maximized. If one's scale is fitness, that is, there would never be a threshold and there would always be a tendency to climb up. If one's scale is some part of fitness then satisficing would often come into play, I would think.

Wimsatt: I was thinking really of something else. You mentioned the importance of specific advantages for dealing with complexity, or specific regularities that emerge when dealing with complexities, and I wondered whether you had had any interaction with Simon's ideas on this.

Van Valen: Yes, I've been interested in his work on this. I haven't found any direct relevance to evolutionary processes - he deals with quite different sorts of processes, but his insight is valuable. The sorts of regularities with respect to complexity that one gets in broad-scale evolutionary considerations are as far as I know quite different from those one gets in broad-scale considerations of human interactions. Perhaps there are similarities, as there are phenomenologically; I have not really found them.

Clive Sattler, McGill University: You invoke the notion of Aristotelian teleology. I don't see why this is necessary and I also don't see how this works because as far as I know Aristotelian notion of teleology implies the notion of final causes and I don't see how in natural science we can use the idea of final causes - how it would work.

Van Valen: The reason that I consider this notion useful is, I think, the same reason that Aristotle did - an eye is made for seeing, a lung is made for breathing. In development, and Aristotle did some work in development, it develops from effectively nothing, nothing visible as a real, functioning structure. This development, of course, is programmed, and the reason that it can occur is by the fact that environments are predictable: our ancestors had need for sight and the environment is sufficiently predictable that we still do. By natural selection operating in the past the result is what I believe Aristotle called teleology. It is not what is now usually called teleology as a result of Christian tradition. This is perhaps a difference in interpretation of Aristotle rather than of biology.

George Oster, University of California, Berkeley: I'm sure I misunderstood you and maybe you can set me straight. Did you mean to imply that conservation of energy puts any serious constraint on evolutionary processes? Maybe you can explain what it was you did mean. You said something about conservation of energy implied that evolution was a zero-sum game.

Van Valen: I deny saying that, or if I said I regret it. What is your question, then?

Oster: What is it that makes evolution a zero-sum game?

Van Valen: Oh. The existence of a certain amount of available energy to degrade. There's only so much energy coming down in sunlight for plants to use. There is



only so much energy that plants fix that can be used by heterotrophs and this amount of energy is then partitioned among the heterotrophs and if one heterotroph, be it fungus or anything else, gets more there is less left for the rest of the community.

Oster: But that's the First Law of Thermodynamics. Are you saying that that puts a constraint on evolution?

Van Valen: Yes. If there was not a constraint like this then life could evolve pretty much in the absence of competition and one would eventually come to some thermodynamic limits I suppose, but life is very far from them. This isn't really an aspect of the First Law because it doesn't consider the flux of nontrophic energy.

Oster: Okay, I guess what I'm saying is - I certainly don't disagree with the First Law of Thermodynamics, but what beyond a trivial conclusion that alludes to growth can you get from that?

Van Valen: The main innovations in this approach are, first, the interpretation of evolutionary fitness in terms of energy, and secondly, the view of evolution as largely a zero-sum game. Most of the consequences of these views don't differ from ordinary theory, which should be encouraging. However, some do differ. I have discussed a variety of such differences in four papers (Van Valen, 1973, 1974a,b, 1976b) referred to in the manuscript of my talk.

Anatol Rapoport: Am I not right in supposing that only a miniscule part of the total energy coming from the sun is utilized by the total organisms? If that's the case then where does the constancy come in? It's possible to envisage a cooperative game in which all of the organisms join together in order to get more of the available energy from the sun. Where does the zero-sum game come in? If there is a practically infinite supply of energy, that is, relatively speaking, because a very small part is actually utilized, then it's a logical non sequitur. It may very well in fact be a zero-sum game but it's not logically compelling to call it so, if in fact the amount of energy utilized is only a small part of the total. That's my first point. I'll just make another point, and that is there are zero-sum games that are two-person zero-sum games. Also others which are n-person games. Now, in a two-person zero-sum game, it's indeed the case that the sum total of all the wins and losses balance each other out. However, any subset of the n players can nevertheless enter into coalition with each other in order to get more of the total available supply than the others. So it is, from a logical point of view, the n-person zero-sum game offers an entirely different possible dynamics than the two-person zero-sum game.

Van Valen: There is certainly much unused energy, but given such constraints as absorptive spectra of photoreceptor molecules, and shortages of other resources such as water which limit the use of energy, it is difficult to see much more that organisms can do. And if they can, they would; this is the critical point. Mutualisms exist but, as I noted in my talk, in the context of coalitions in the zero-sum game. Coalitions can originate in diverse ways. Such phenomena as the colonization of the land, or the origin of lichens, are real exceptions but (like glaciations or marine transgressions) merely establish new equilibrium levels within which the zero-sum game continues after the interruption. Very local areas do change their energy fixation over ecological time-scales, but this is averaged out over either slightly broader areas or slightly longer times. And in probably most such cases the amount and rate of change makes a zero-sum game a suitable approximation even very locally. However, I am not persuaded that game theory in its present restricted form is an adequate formalization for more than a small subset of the conflicts in the real world, human or natural. I am nevertheless optimistic that the theory can be appropriately extended. There are several directions for such generalization to go, and my presence at this conference is mainly to motivate such work.

Chris Plowright, University of Toronto: What I found confusing about all of this last part is that it involves ambiguities in the concept of limitation, and I would like to ask a specific question. I'd like you to distinguish between the use of the words limitation and regulation. Ecologists perhaps today are in uneasy possession of generally recognizing that competition can occur only where some or other resource is limited, but any precise form of limiting is still far away and I would like to hear something on that from you.

Van Valen: Yes I do distinguish, and quite sharply, between density-regulating factors and limiting factors. Perhaps this is best seen by an example. Temperature is not a density-regulating factor, except indirectly by its effect on other factors, yet it can directly limit the distribution of a species. So temperature can be a limiting factor in this sense but not a regulatory factor. The distinction is like that between rate of population growth and equilibrium population size. Many factors are, of course, both regulatory and limiting, but in any given population only some subset of these, and in my view probably a very small subset, usually only one, is directly effective in determining the range of sizes or densities that the population actually undergoes.

Plowright: Can you prove that?

Van Valen: No, I cannot prove it. It is my interpretation of available evidence and some other people have different interpretations, I realize. We need much more evidence as to what in fact regulates populations in nature, and it's hard - the study of this even in one case is hard, so collecting the data for consideration of a population of these cases is difficult. One cannot simply look at one factor and say - aha! it's density dependent in the appropriate way and therefore it's regulatory, because it may be insufficient to produce a regulatory effect. This is a problem with some studies that have been done. I don't want to go into this. The problem is difficult and I cannot prove that assertion.

Question: I would like to ask all three panelists what their opinion is of cooperation in nature - more specifically, what they think about the idea by the Czech zoologist Novak, who claims that cooperation plays a much greater role than competition within species whereas competition plays a great role only between species. He thinks that generally the idea of competition should be more applied between species than within species and that even Darwin has been misrepresented and misinterpreted in this respect.

Van Valen: Well, maybe it would be that any cooperation could be a mechanism of competition, that one has to look in any instance of cooperation as to what is gained by the cooperating units at the expense of some other units and whether cooperation is more important within species than among species. I don't know. I suspect it's true because it's easier to evolve (one can see more possible mechanisms), but on a factual basis I have no real opinion.

Plowright: I'm very reluctant to say anything about this at all because I'm paid to say lots about it during the year. I think I'm a general open-minded sceptic. I think I'm most interested in continuing to probe the necessary conditions under which group selection can act and I don't regard this in any sense a closed subject; I'm certainly not the best informed person on the general literature around this. I assure you to the extent that group selection is possible and, of course, in my little corner of the world, the social insects, we have nice examples where the possibility of different levels in the hierarchy can be important, but I think the onus is still more on the proponents of group selection to demonstrate it. I liked hearing what Anatol said yesterday, but on the other hand there are formidable obstacles about postulating group selection.

Wimsatt: I'm, I guess, a somewhat sceptical advocate; that is, any discussion of this has to really proceed from the publication of George Williams' book of 1966. That, and shortly thereafter, probably represents the high-water of scepticism against any higher-level unit of organization. I think actually if Williams were taken at face value he has problems explaining why individual genomes or individuals are units as opposed to individual alleles, and I think there are serious problems

with it at that level. I think there is progress, and I want to agree with both previous speakers and what they said. Leigh basically clarified what he meant by the role of cooperation in competition and Chris said he wants to see more conditions under which it does or doesn't operate. Presumably it does or doesn't, depending upon the relative magnitude of dynamic forces at different levels of organization. We've made at least progress from Williams' time in that we have now less of a tendency to rule out a priori the possibility of selection happening at higher levels of organization.

Van Valen: I've published two or three examples myself - one dealing generally with dispersal (Van Valen, 1971), the other one or two dealing generally with body size, with data for real examples (Van Valen, 1975a).

Question: To change the subject again, this is really just taking off from something Dr. Van Valen said when I talked to him a little bit earlier. It seems to me that his idea of a zero-sum amount of energy to partition makes a particularly powerful argument with respect to the effect of man on the rest of the natural world, because man's increase in numbers and in the use of energy must represent a tremendous perturbation within a limited amount. Therefore, there's got to be reduction in the rest of the natural world. Those of us who are interested in conservation are often concerned with vanishing species or rare species. In trying to preserve them, then, in face of having smaller and smaller total energy available for them, we're really attempting, it seems to me, to increase the number of rare species relative to these communities. I wonder if this is a valid possibility. I don't know whether the panelists have anything to say on this or not.

Van Valen: Well, perhaps rare species can be increased by artificially manipulating the environment. I don't know what else can be said beyond this. As Homo sapiens or any other species becomes more abundant it uses a much greater part of the world's resources. Then other species suffer, yes. This is another argument for stopping our population growth and for reducing the number of people.

Plowright: Well, I don't agree with the zero-sum hypothesis in the first place but I'd like to say that when you start talking about conservation you're talking about entirely different rules of procedure. I think the simplest case to point out is if you applied water to deserts you can greatly increase the utilization of the solar energy falling upon those deserts, etc., etc., so I don't see any easy way to answer the question you've posed.

I was made very uncomfortable by Leigh's use of the blood-group example, which of course depends upon differential population growth in different parts of the world. This is purely a propaganda statement that I'm making and the conclusion that this is a demonstration of the increased fitness amongst some groups on a global scale I find a very uncomfortable conclusion indeed, as a long-term advocate of population control.

Van Valen: We are not in disagreement on this point. The fitness increase is perhaps temporary, perhaps permanent, because we don't know what will happen when the crunch comes.

Plowright: Maximean rather than maximin, eh?

Van Valen: On the short-term time scale, yes.

Roger Hansell: I have a question for Dr. Van Valen, who is not here to defend himself. Would anyone like to take on the job? Does anyone understand what the relationship between the constant energy supply which he postulates, and the utility for fitness, is? Does anyone here have that clear in their minds?

John Maynard Smith, University of Sussex: I'm not really able to defend Leigh on this, but I do think that there is a reasonable approximate line of argument from a constant energy supply and a constant rate of extinction, which is after all the observational things that Leigh wants to get to. I mean he starts, after all, with the empirical observation of an approximately constant rate of extinction for a given taxon and a given environmental situation, and he tries to deduce this

through some sort of zero-sum assumption. I believe that he can do that with some validity, and after all we're not going by the constancy of light or something, we're talking about something that's constant within a factor of two. I think that Leigh's argument is perfectly valid if you start from the idea that an approximately constant rate of input of primary production in an ecosystem as a whole, and a constant species abundance distribution of the kind of economical distribution of pest or something, then I think that leads him not unreasonably to the assumption that there's a constant rate of extinction of species. Where I would part company with him is calling this fitness. Fitness is a technical term and it doesn't mean that. In his first formulation in evolution theory he spoke of fitness as if he actually meant genetic fitness and he talked about each evolutionary advance by each species being experienced as a deterioration of the environment by all the others and a decline in their fitness. I would accept the whole of Leigh's argument, but I would prefer him not to use the word fitness, but something else. But if he doesn't mind altering the word I would have thought his argument was great.