ENERGY AND EVOLUTION

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ABSTRACT: Energy causes evolution just as it causes other processes. I define natural selection and fitness wholly in terms of trophic energy; expansive energy is energy used for growth and reproduction. The proposition that natural selection maximizes expansive energy is proposed as the third law of natural selection. Surrogate resources are resources whose acquisitions is selected for as a way of getting more energy. Expansion, change in size of persisting units, is a previously unrecognized component of fitness, which permits the conceptual reorganization.

Time scales are fundamental in evolution. For instance, group and individual selection can mostly be reinterpreted as a difference in time scale. This and other distinctions such as maximin vs. maximean strategies, or adaptedness vs. adaptatility, can thus form continua rather than dichotomies. The use of energy makes all forms of natural selection commensurable and permits unified analyses at all levels.

Two arguments each conclude that competition for trophic energy is important in all or almost all communities, with special reference to clams. I also refute all available arguments for competition being unimportant among clams. Worldwide trophic energy seems to have been roughly constant for 10^9 years or more.

The amount and pressure of competition reflect the effect of competitors on populations and individuals respectively, and have different consequences. The line of expansive sufficiency demarks the favorable and unfavorable regions of the adaptive space, the regions where the species or average individual does or does not control enough energy for expansion. This expansive energy is an important part of the force of expansion of a species at any point in the adaptive space. The competitive ability of phenotypes varies with environmental variables and a general form of the principle of competitive exclusion emerges.

The different selective pressures in the favorable and unfavorable regions produce central and marginal selection, but because of energetic subsidy of the unfavorable region both kinds of selection are often important for most individuals. A selective response to competition always involves a reduction in overlap or an increase in competitive ability. It usually results in an increase in competitive pressure, while the amount of competition may change in either direction.

High- and low-pressure competition characterize different kinds of habitats and species, and the selection associated with each has different results. Competitive pressure measures the effective difference in adaptations, so clams are adaptively more similar to each other than are mammals. Low energy availability, and an adaptation to it, may itself be a major cause of the great diversity of species on the floor of the deep sea.

Regulatory energy, the expansive energy consumed by population regulation, emerges as the best measure of fitness. The four ways of increasing regulatory energy exhaustively partition natural selection. About 2 percent of the trophic energy of both modern man and a palm is used as expansive energy; the realized fitnesses of both species are similar.

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INTRODUCTION

Ecology and population genetics have developed largely in isolation from each other. Population biology is still more a mixture than a fusion. The intergradation that occurs is relatively superficial, being grafts onto pre-existing theories. Yet a feeling persists that the actual processes are some-how more unified than the theories. One purpose of the present paper is to indicate how these disciplines are deeply interconnected, so that a separation is as artificial as one between cytology and transmission genetics.

My main purpose, however, is to begin a reconceptualization of evolutionary theory in terms of energy. This is evolution considered as a process; what evolves, however, is the phenotype and its variation, and the phenotype is development. Evolution is the control of development by ecology.

Energy drives evolution just as it drives physiological processes. I am therefore trying to obtain a causal account, even if an elliptical one, not another descriptive account from another viewpoint or in another restricted domain.

If you like, this is a different theoretical paradigm, even though most existing theory carries over unchanged except in how one interprets it. This is similar to the situation with different foundations of mathematics. An approach based on energy seems, however, to give more theoretical power as well as to reflect causality. The shift in outlook has been difficult for me and has involved several stages. Probably others, especially geneticists, will find it no easier. However, any theory which one finds uncomfortable but for which one cannot say exactly why, deserves serious consideration. Such an uncomfortable feeling signals a challenge to one or more of one's unexamined, and perhaps unjustified, assumptions.

Numbers in parentheses, except equation numbers, refer to notes at the end of the main text. The paper is complex because the subject is complex. I have tried to put qualifications and branches of the argument into notes. The notes are not subsidiary but their content distracted from the flow of the paper when the one-dimensional constraint of writing constrained them also in an earlier draft.

THE RED QUEEN'S HYPOTHESIS

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_2 and hydrogen from H_2O. 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 per cent 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 (1). For heterotrophs as for green plants, what one gains, the rest lose (2).

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.

ENERGY AND FITNESS
Fitness

Fitness is the central concept in population genetics. But there is widely felt to be a worm in the apple barrel, or perhaps the barrel has no foundation at all.

Among evolutionary processes, fitness is nonrandomly associated only with natural selection. It is therefore reasonable to consider fitness as what natural selection maximizes, and this is indeed a common view. But what does natural selection maximize? Here we find a whole can of worms.

A few are easily digestible. Natural selection operates at different levels, on haploid gametes as well as on the diploid individuals that result from their fusion, and its direction may differ at different levels. We just need to recognize that each level can maximize on its own and so has its own determinants of fitness. Selection at any level can be detrimental as viewed from any other level. This is well understood by some (3).

All else equal, natural selection maximizes viability. All else equal, it maximizes fecundity. And mating success, and colonizing ability, and trophic efficiency, and development rate, and escape from predators, and much else, at many time scales together. How, in actual fact, is the resultant of these mutually conflicting components determined in nature? Population genetics says that selection maximizes the number of individuals, usually in the next

generation. Lewontin (1961) thought it maximizes the lowest probability of
survival of any offspring after one generation; later (1968) he thought it
maximizes stability. Mac Arthur (1962) and Slobodkin (1972) thought it maxi-
mizes efficiency, although their meanings of efficiency were quite different.
Thoday (1953) thought it maximizes the probability of any descendants after a
long period of time. Carson (1961) thought it maximizes biomass. Claringbold
and Barker (1961) and perhaps Darwin (1859, pp. 336-337) thought it maximizes
competitive ability. Birch (1960) thought it maximizes the actual rate of
increase in the number of individuals in the population. Levins (1970) thought
what it maximizes depends on specific circumstances, although he seemed to
assume some unspecified sort of ultimate criterion of survival of descendants.
Lotka (1922) thought it maximizes the total energy flux through all organisms
jointly. These statements merely sample the diversity of views available,
which are on so basic a subject as to determine the nature of the theories in
which they are embedded. One can't use standard equations to answer the
question, because equations already have built-in assumptions that determine
the outcome. Ones assumptions must be true and complete for this method to
work. The question is one of fact and can be answered only by examination of
actual processes.

Natural selection is a single process which always gives an unambiguous
result under defined conditions. Natural selection is also a simple process,
and it is curious that it causes so much difficulty. This might lead one to
suspect that the situation is poorly formulated. I believe this is the case,
and have defined the realized absolute fitness of any evolutionary unit roughly
as its control of trophic energy. In a later section I will make the nature
of energetic effects more precise, but the critical point here is the replace-
ment of number of individuals by energy control. I will try to motivate this
replacement in two ways.

Energy and individuals

First, consider two seedlings of a grass. Each spreads by tillering to
occupy a field. In one field the tillers are retained; in the other they are
lost. Genetical theory would call the second population and its genotype
vastly more fit because there are many more individuals. Yet there is no more
than a trivial biological difference. Degree of connection has no sharp
demarcation and we can't get around the quasi-problem by calling each shoot an
individual; what then should we do with a bush? The natural solution is eco-
logical. As a general proposition, how the energy units of a population are
partitioned among individuals is a matter of secondary importance. Energy
control is causal and numbers per se are not.

Secondly, 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 (4). 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.

Expansion

Thus we see here in pure form a previously 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 bounded 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 (5).

Expansion is unimportant in individual selection and therefore is not part of existing theory. All individuals die (or divide), although their expansion can be relevant for clones or even trees. Expansion is much more important on the group level. Here the unit of selection is the group, even if not sharply bounded. Some groups survive indefinitely, and their change in size is of evolutionary importance. We all have Precambrian ancestors. Such groups have greatly expanded. Numbers are inversely related to body size. One group might get a much larger body size, outcompete all other groups in its trophic level and habitat off the face of the earth, and still have fewer individuals than before even though it controls much more trophic energy.

So energy control is more important than number of individuals. It is easy to see historically how a belief in the paramount importance of individuals arose. Genetics is simpler to deal with than ecology is, in formulating precise theories. Whether for this reason or others, genetics rather than ecology became the basis of modern evolutionary theory. Breeding experiments are carried out among individuals of about the same size and energy use, so the inadequacy of the individual as a unit in a broader framework is usually overlooked. If ecology had developed as a science 30 to 50 years before genetics, instead of the reverse, orthodox evolutionary theory might be rather similar to the approach of the present paper.

If we realize that death and extinction are the extreme case of negative expansion, all of evolution can be considered as sustained differential expansion. From this viewpoint, reproduction occurs within, rather than by, the units whose expansion is being considered. For genes, the units (the sets of individuals with the alleles considered) usually are mutually overlapping. For phenotypes, the units often intergrade with each other to form continuous variation. They are then fuzzy sets (Van Valen, 1964; Zadeh, 1965), to which the same analysis applies.

Energy as causal

Number of individuals may not be all-important, but why substitute energy control in particular?

Potential energy in the form of reduced carbon is the fuel of the fire of life (6). All other resources, even when regulatory, can be considered surrogate resources (7) 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.

Phosphorus is sometimes thought central for aquatic communities. It probably does often regulate the abundance of blue-green algae and so the total productivity of some communities. Moreover, Broecker (1971) notes that "plants now consume and send to the deeps more than 95 percent of the available P" in the euphotic zone of the oceans. But the brachiopod Lingula has a phosphatic shell; it competes successfully for the phosphorus with algae and other organisms. This degree of control of phosphorus isn't selected for per se; any other suitable material would do as well, and most shelled organisms do use other materials. Not so with reduced carbon: any organism that can effectively obtain and exploit it will do so. Some have an excess of reduced carbon because other factors prevent its full use. Shortage of nitrogen often does so for aphids, shortage of space often does so for barnacles (8), and predation does so for prickly pear in Australia, where the regulatory resource is absolute space (9). But if such species can reduce the effect of these interfering factors they always are selected to do so (10). Space will be lost if energy is thereby gained (11). Such priority is not always given to something like phosphorus or resistance to predation. Predation is minimized, but not to the extent that a reduction overly interferes with aspects of competitive ability. Control of trophic energy decides where each such balance occurs. Trophic energy is the arbiter among competing strategies of adaptation.

For green plants the situation is slightly more complex, as their trophic energy comes from both sunlight (gross production) and their own previously reduced carbon. Whatever of either kind they can control for metabolic functions, they do. Metabolically (and therefore reproductively) inaccessible carbon, as in wood, is thereafter irrelevant to the plant's computation even though the plant may need to spend energy to make and protect its wood so that it may gather the more energy from the sun. Some organisms are partly heterotrophic and partly autotrophic. Insectivorous angiosperms gain nitrogen (but don't discard the carbon), which permits them to grow and reproduce more and so get energy. Reef corals, planktonic and large benthic foraminiferans, lichens, and even all green plants if chloroplasts originated endosymbiotically, are ecological units (species) with double and widely divergent ancestry, exemplifying reticulate evolution on a grand scale. All retain their autotrophic heritage and most retain their heterotrophic heritage. They show that heterotrophs can find it advantageous to evolve to autotrophy, as flagellates and dodder show the reverse. The advantage in each case is a net gain of trophic energy.

As Hairston, Smith, and Slobodkin (1960) noted, "If virtually all of the energy fixed in photosynthesis does indeed [get used by organisms, as it does], it must follow that all organisms taken together are [ultimately regulated] by the amount of energy fixed." And as Egbert Leigh commented at this point, if phosphorus were absent life could probably evolve without it. But if the sun and its energy were absent, no life of any kind would be possible.

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.

A plant in a desert, where energy from sunlight is in great excess, still maximizes its control of that energy. It does so by maximizing its control of water or of whatever happens to regulate its population density (which is almost always better measured in units of trophic energy flow than in units of individuals). If gaining more water didn't give it more usable energy, it wouldn't gain more water (12). Many kinds of such surrogate resources exist, for different organisms and habitats, but the extent of their direct control is in every case subsidiary to their ultimate effect on control of trophic energy.

Expansive energy

The trophic energy controlled by an individual or species per unit time, e_c, is composed of energy that is directly productive (e_d), waste energy (e_w), structural energy (e_s), and reserve energy (e_r) that is not ingested:

$$e_c = e_d + e_w + e_r + e_s. \tag{1}$$

The partitioning is to some extent arbitrary and conceptually overlapping, and other partitions are possible (13).

Structural energy is that part of earlier "production" (the energy contained in the materials of an organism's body) which is unavailable for reproduction. Some of it is usually available for maintenance. Reserve energy is external energy that is unavailable to competitors because it is defended, as by territoriality or allelopathy, but is not now used by the referent unit (14). Waste energy comprises egesta and excreta of all kinds (15). Similarly,

$$e_d = e_m + e_e, \tag{2}$$

where e_m is maintenance energy and e_e is _expansive energy_, the energy available for growth and reproduction (16-18). Expansive energy can be equated with _fitness_.

It is important to note that these quantities are measured per unit time (19). In other words, they are effectively rates. e_e for a population is a net rate of increase rather like r_t (20): where b is biomass expressed in energy units for a uniform population of size n (21), then at optimal and suboptimal densities

$$e_e = \frac{1}{n}\frac{db}{dt}. \tag{3}$$

At higher densities part of e_e is consumed by density-dependent effects.

Waste energy will be reduced by natural selection only if it thereby increases expansive energy at the time scale of selection one is considering. The same is true for the other components. Maintenance energy is necessary for survival so that growth and reproduction can occur at all. Because of such interrelations among the components, mediated by natural selection, total control of trophic energy will ordinarily change in the same direction as expansive energy (22).

LAWS OF NATURAL SELECTION

Natural _selection_, _at_ _any_ _level_ _or_ _time_ _scale_, _maximizes_ _the_ _expected_ _amount_ _of_ _expansive_ _energy_. This proposition follows trivially from a revised concept of natural selection, which I develop below. Mitchell and Downhower (1974) regarded "trapping energy as the essential element for existence," although they still interpreted fitness in terms of numbers of individuals. Simpson (1949, p. 121) said that ". . . the most nearly general features of the record [are] the 'barrel-filling' effect, or the principle of total increase (with the concomitant tendencies to expand the barrel and to refill when emptied at any point)." Lotka (1940) said that "that particular aggregation of such organisms, of such energy transformers, will be most favored for growth (at the expense of other similar aggregates, it may be), whose

activities, under prevailing conditions, are best adapted to bring into its grasp and control the energy required to conduct these activities." Maximization of trophic energy control is a more precise statement of the same approach.

The above proposition may be thought of as the third law of natural selection. The first law is Fisher's Fundamental Theorem; the second law is Wright's purely genetical principle of maximization of his $\bar{W}$, $\bar{W}$ being the expected relative number of offspring in the population in the next generation. Each of these two laws has been claimed to be false, but their problem is merely that their domain of truth is less than universal (cf. Wright, 1969; Crow and Kimura, 1970; Price, 1972; Svirezhev, 1974). The third law is also restricted, as I discuss below.

Is the third law true?

To see that the third law is true we can derive it deductively, the truth of the law then depending on the truth of the premises. We can decouple energy from numbers and see which is effective. We can consider the components of selection piecemeal. And we can examine cases which might seem to contradict the law.

I defer the deduction until I discuss natural selection itself. I have already considered the decoupling of energy from numbers but give two other examples. First, it should be clear that in the real world natural selection does not decrease body size, even though this would produce more individuals, when such a decrease would also decrease the amount of expansive energy (and trophic energy control) of the population. Secondly, for individuals with the same body size, endotherms use energy at a rate several times that of ectotherms. In units of trophic energy, one endotherm equals several ectotherms. Yet endothermy has evolved at least twice. Its origin is known to have been gradual for mammals (Van Valen, 1960), although we don't know what happened to population sizes. It is easy to see, however, that given the common advantages of a high body temperature (Hamilton, 1973) endothermy could evolve even if the total energy available to each lineage was constant. The more endothermic individuals would survive and reproduce better than the more ectothermic ones, and the population size and $\bar{W}$ would decrease.

The components of ordinary individual selection can be exhaustively partitioned into viability, reproduction, and generation length. A dead individual has no more offspring or metabolism and thereby loses future expansive energy and energy control. Greater reproduction, whether by the individual in question or its kin, is immediately greater expansive energy, and gives greater energy control to the set of offspring. And a shorter generation length gives more generations, and therefore greater potential reproduction and expansive energy, per unit time. Thus, whenever individuals are energetically equivalent to each other, the ecological approach reduces to the genetic approach. And therefore, in the domain where natural selection maximizes $\bar{W}$, it also maximizes expansive energy.

With group selection, including selection at the level of species and higher, the same components occur and an additional one enters. Death is extinction, and reproduction is the founding of new populations by dispersal or the branching of lineages. Expansion, the additional component, obviously involves energy. Therefore all components of selection can be expressed naturally in terms of energy, and the action of each leads to an increase in expansive energy (23).

Before I formulated the third law in its present form I thought it had exceptions, so my original proposal of it (Van Valen, 1973a) was only as an

approximation. However, the apparent exceptions are spurious and I have found
no real ones. For instance, interference competition can decrease the absolute
expansive energy of both competitors, yet even then interference can originate
and persist. It is to the advantage of one competitor initially to interfere
with the other; the first competitor gains more energy than before. The
second competitor then gains energy above its new low level by interfering
with the first. Both the first and the second may now be below their original
levels. The local maximization is for each competitor individually, as it
perceives its own immediate world, not for the joint system. Each competitor
loses by abandoning its own interference unilaterally, and the competitors
can't communicate with each other rationally. This is an example of the
Prisoner's Dilemma of decision theory (Rapoport and Chammah, 1965) and depends
on the absence of effective communication between the competitors. The
language of this paragraph applies whether the competitors are individuals,
phenotypes, genotypes, species, or higher taxa. A more interfering phenotype
within a species wins relative to a less interfering phenotype but may lose,
in part, relative to a formerly subordinate species that can now expand to
control the energy the phenotypes of the other species relinquish.

Natural selection

I now show how a revised concept of natural selection follows naturally
by an obvious modification of the existing concept. For simplicity I con-
sider selection for one generation on two units such as species or monoploid
alleles. Their initial frequencies can be called p and q; $p + q = 1$. After
selection, the relative frequencies are $p(1 - s)$ and q. Normalizing these
values to give a sum of 1 requires dividing each by $[p(1 - s) + q]$, which is
the same as $[1 - ps]$. This is the standard treatment. If we use absolute
frequencies, as is occasionally done, we eliminate the constraint of summing
to 1 and therefore eliminate the division by the sum, although the time inter-
val is still a full generation. The selection coefficient s is then the
proportion that the change is of the original number of individuals. There
will in this case ordinarily be a separate selection coefficient for each
alternative unit. In a finite world it makes sense to call this process
selection (24), and it seems to be recognized that, although involving more
parameters and the genetically awkward concept of population regulation, the
case of absolute frequencies underlies that of relative frequencies.

Then (25) we simply replace numbers of individuals by their control of
trophic energy. The selection coefficient is then the proportion that the
change is of the original energy control.

<u>Natural</u> <u>selection</u> is the action of fitness in causing differential expan-
sion. We recall that realized fitness is expansive energy. In situations
like balanced polymorphism, the differential expansion may occur for only
part of a generation before being cancelled by some other process.

The domain of any instance of selection is crucial with respect to both
time and the location of the energy, and disregard of this point can give
serious misunderstanding. For instance, to take an extreme example, a tree
expands and controls more energy as it grows into the canopy, and thereby
gains expansive energy both absolutely and relative to its still suppressed
neighbors. This process satisfies the definition of natural selection. We
think it strange that it does so, but only because we are unaccustomed to
thinking of expansion as a component of fitness. If the tree doesn't reproduce,
other phenotypes will control its energy later, but until it dies it does in
fact control its energy and it will have some expansive energy until near
death. The arbitrariness of any time scale of selection is also relevant.

Expansion is important for groups and for clones, even connected ones, and there is no evident natural way of distinguishing these cases from that of the tree, or even a real motivation to do so. Defining natural selection in terms of energy liberates it from the traditional paradoxes of fitness.

The maximization of expansive energy is of an expectation, in the statistical sense, which may or may not be realized in any given case (26).

Domains and deduction of the third law

A formalization of the deduction of the third law seems unnecessary; its structure is as follows. By the definition of natural selection, differences in expansive energy cause differential expansion. A unit with more expansive energy than another unit has greater expansion, i.e. its increase in control of trophic energy is greater or its decrease is less. But greater control of trophic energy results in greater expansive energy. Therefore there is a positive feedback. However, there is an externally imposed limit on the amount of trophic energy which the unit can control, and so a limit on its expansive energy. Therefore the amount of expansive energy is maximized rather than increasing indefinitely. Because of the restriction on total trophic energy control, an equivalent statement is that the maximization is of the proportion of trophic energy control that is expansive energy. The deduction is nearly the same for both the absolute and the relative cases (27). As the statement of the third law implies, the time scale of maximization is the same as that of the selection being considered.

The domain of truth of the third law has at least five restrictions in addition to that of time scale. Natural selection must be the locally predominant evolutionary force: dispersal or other forces can offset the effects of the law if they predominate. Secondly, interference among different units must be insufficient to outweigh the effect of the law. Thirdly, when we consider selection at or above the level of the individual, prezygotic selection must be negligible. However, some kinds of sexual selection fall into the domain (28). Fourthly, greater control of trophic energy must in fact lead to greater expansive energy. This is untrue, for instance, for a senescent tree whose needs for maintenance and growth have risen too far (29).

Finally, with other laws of natural selection, the domain of truth of the third law requires that the environments before and after selection (or the part of the selection being considered) are sufficiently similar. A favorably selected phenotype may be poorly adapted to a new predator or a drought. Similarity of the environment is necessary for heritability of fitness and thus for any response to selection. How robust the selection is to environmental change lacks a general answer. The fuzziness is ontological, not epistemological, although it is quantifiable at a proximate level by means of the heritability of fitness. The fuzziness is a necessary aspect of the boundaries of the domain of truth of the law. There must be enough similarity in the environment, or in the pattern or nature of environmental change, for natural selection to be adaptive in any useful sense (Levins, 1968).

The third law, like the second, determines which phenotype or genotype will be selected. Where the domains of these laws coincide, they seem in every case to give the same result. The third law is more than a formal statement. It expresses the driving force of evolution. Darwin was familiar with this force, but didn't express it explicitly in terms of energy: "Thus it will be in nature; for within a confined area, with some place in its polity not so perfectly occupied as might be, natural selection will always tend to preserve all the individuals varying in the right direction, though in different degrees, so as better to fill up the unoccupied place" (Darwin, 1859,

p. 102). Bertrand Russell (1927, p. 27) also noted 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.

Whether natural selection involves absolute or relative amounts of energy
is a matter of convention only (30). It does both at the same time, always.
A "nonselective" agent in one domain is selective in a larger domain. A pond
fills in and all aquatic species may be nonselectively reduced and eliminated.
But terrestrial species gain by the process, which thereby selects for them
and their properties (31). A phenotype may increase in a species which is
declining to extinction. Here the direction of selection of the same pheno-
type depends on the domain one is considering. Population genetics ordinarily
gives an increasing fitness to the relatively increasing but absolutely de-
creasing phenotype. In terms of real biological causation we can combine
selection in different domains and make them all commensurable. Evolution
within species is naturally tied to evolution among species and can be
measured in the same way. Energy control is thus a unifying principle.

TIME SCALES IN EVOLUTION

There is no natural time unit in evolution, and natural selection operates
on many time scales simultaneously (32). One generation isn't a magic unit,
most obviously because organisms with different generations interact, even
within many populations (33). The difference between individual and group
selection is to a large extent one of time scales except for David Wilson's
mechanism (1975), where the selected populations form and dissolve in less
than a generation and so the process has the time scale of individual selection.
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
(34), and is Wynne-Edward's 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 (Van Valen, 1971a) and other group-selected features,
the time scale can be interchanged with the level of selection.

A phenotype that uses or controls more trophic energy than another can have
other disadvantages that lead to its having less expected use or control later.
By submergent behavior (Maiorana, 1976) some animals minimize food gathering
so that they also minimize predation. This is an aspect of the effect of
different time scales on natural selection, but it brings in explicitly the
existence of costs and benefits for different strategies. At different time
scales the costs and benefits may differ greatly. The existing strategies
are determined by the time scales that have been most able to influence the
evolution of the population, and there is clearly no single generally applicable
weighting even though patterns may be obtainable from history and the nature
of environmental fluctuation.

A reluctance to consider trophic energy as the ultimate arbiter of evolu-
tion is perhaps related to the unimportance of expansion as a component of
fitness at the individual level. However, we have seen that this unimportance
is merely a matter of time scale and so has no fundamental implication.

As is well known, an immediate selective advantage can be disastrous over
longer intervals. I have analyzed some cases of this sort (Van Valen, 1975a).
Here the results of selection varies depending on the interval one considers.
At a low level, the "grandchildless" mutant of Drosophila subobscura has no
known selective effect on its homozygous carriers or their offspring except to
make the latter sterile. There is thus no decrease in realized fitness for

two generations. This interval is therefore the one best suited to considera-
tion of selection on grandchildness unless one is really interested in only a
one-generation comparison. There is nothing paradoxical about natural selec-
tion 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

$$F = \int_0^\infty w(t)e(t)dt, \tag{4}$$

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. If $\int_0^\infty w(t)dt = 1$, then Equation (4) gives
a weighted average of expected future expansive energy, for each weighting
function (35). Equation (4) is modified from Van Valen (1973a). If one is
interested in the fitness after some specific interval t, then of course $e(t)$
gives a conceptually unambiguous measure.

   The difference in $e(t)$ over different lengths of time is critical in
evolutionary strategies. Such strategies are themselves selected for and are
of prospective use only as a byproduct. Short-term evolution maximizes the
expected expansive energy rather closely, but in long-term evolution extinc-
tion is more important. Strategies close to the maximin extreme of Lewontin
(1961), where bare survival is all-important, are developed on the time-scale
of extinction even though continually eroded by short-term development of
adaptations that give a maximean strategy before extinction (36).

THE CONSTANCY OF TROPHIC ENERGY

   Until very recently one could only guess whether the rate of net photo-
synthesis (and therefore trophic energy for heterotrophs) through geologic
time has been similar to that now. Pronouncements are occasionally made on
the topic, but they are based on inferences as to the number of species present.
As we may see in eutrophically polluted waters or, conversely, in the deep
sea, more trophic energy doesn't itself result in more species.
   Jackson (1975) plotted the concentration of humic matter in sediments
from much of geologic time and found a dramatic increase in the Phanerozoic.
His preferred interpretation was a similar increase in biological productivity.
However, all four of his post-Paleozoic samples were from unusually organic-
rich sediments, including a commercial oil shale, unlike all of his pre-
Permian samples. This bias removes any possibility of interpreting his later
data. His earlier data do suggest an increase by a factor of about 2 per 10^9
years. Ronov and Migdisov (1970) found,for rocks of the Russian Platform, a
mean increase of the concentration of reduced carbon by a factor of 3 from
2×10^9 B.C. to the Paleozoic, and a further increase by a factor of 2 into
the combined Mesozoic and Cenozoic.

Whether such secular changes are caused by a change in primary productivity is itself open to question. The efficiency of decomposers would not be expected to decrease over time, at least until the advent of metazoans with fecal pellets. Change within sediments over time is possible, but patterns through time in components of the organic material (Jackson, 1973, 1975) suggest that this effect is minor. A critical assumption, however, is that the same average rate of sedimentation has occurred through geologic time. Ronov's and Jackson's data are for concentration of reduced carbon in preserved rocks, and preserved rocks decrease roughly exponentially with greater age (Garrels and Mackenzie, 1971). The mean rate of sedimentation may possibly have been greater before the colonization of the land, but the available evidence is entirely ambiguous as to whether this did happen. Thus the evidence of reduced carbon does suggest that there may have been a very slow increase in primary productivity, at least in the Precambrian, but that any such increase was negligible even on a time scale of many million years.

Better evidence on the Phanerozoic situation comes from work by Garrels and Perry (1974). They find that the absolute rate of burial of reduced carbon is indistinguishable from the absolute rate of oxidation of reduced carbon in newly exposed rocks, on a worldwide basis. Because these rocks are tens and hundreds of millions of years old, with a mean turnover of 100 million years or more, I interpret this result to mean that there has been an approximately steady state in the rate of deposition of reduced carbon for at least much of the Phanerozoic. In other words there has been an approximately constant difference between the absolute rate of net photosynthesis and the absolute rate of oxidation, before burial, of the reduced carbon so produced (cf. Van Valen, 1971c). The only plausible way for this constant difference to occur would seem to be an approximate constancy in both worldwide net photosynthesis and worldwide efficiency in use of the trophic energy thus made available. Such a situation does not preclude temporary fluctuations but does require that the worldwide level of photosynthesis be regulated for a geologically long time at about its present value.

A third kind of evidence, corroborating the second, comes from studies of carbon isotopes (Schidlowski, Eichmann, and Junge, 1975). Organic carbon has a lower proportion of ^{13}C than does carbonate carbon because of fractionation by organisms, especially during photosynthesis. By this criterion, the proportion of organic carbon in all sedimentary carbon has been roughly constant for at least 3.3×10^9 years. The apparent small contradiction to the direct estimates of reduced carbon may or may not be real.

If early decomposers were less efficient than later ones, a greater proportion of the carbon reduced in photosynthesis would be buried. Thus a constant ratio of reduced carbon to oxidized carbon in sediments could occur, but it would be purely coincidental. This would have no effect on net production of atmospheric oxygen, which depends on the absolute amount of reduced carbon buried. The ratio of ^{13}C to ^{12}C differs somewhat among organisms, and it is again conceivable that this ratio for all organisms coincidentally increased at the same rate as world photosynthesis. The observed differences among organisms aren't great enough, however, to make a large mean change plausible. The same is true for changes in isotopic composition by chemical fractionation long after burial (cf. Leventhal, Suess, and Cloud, 1975). Thus the available evidence, incomplete though it may be, suggests an approximate constancy in available worldwide trophic energy since at least the middle Precambrian. Only relatively short or small fluctuations are consistent with the evidence.

THE UBIQUITY OF COMPETITION

Competition for trophic energy occurs, and is important, in all communities. (A few physically very extreme communities, with conditions which only one or a few species can tolerate, may possibly be exceptions.) There are two sorts of deductive arguments for this proposition. One partly follows Hairston, Smith, and Slobodkin (1960); the other is in the spirit of David Lack.

Little trophic energy is irretrievably lost. Even in a peat bog about 90 per cent of the carbon from net photosynthesis (and much more of that from gross photosynthesis) escapes burial (Reader and Stewart, 1972), and the overall figure for final burial is a good deal less than 1 per cent of net photosynthesis (Holland, 1973; Sackett, 1964, 1974; Garrels and Perry, 1974; Walker, 1974; and less than 4 per cent even in the Black Sea [Deuser, 1971]). On land, however, fire sometimes oxidizes much of the carbon (e.g. Naveh, 1974; Taylor, 1974; Walter, 1975; Lamotte, 1975) and is more likely to occur when more carbon is available; therefore it is clearest to restrict the argument to habitats where fire is negligible, such as aquatic systems.

Moreover, most or all of what small amount of carbon is buried seems to be in compounds unusually refractory to use by heterotrophs (e.g. Menzel and Ryther, 1968, 1970; Deutsch and Cook, 1973; Aizenshtat, Baedecker, and Kaplan, 1973; Stuermer and Harvey, 1973). Therefore heterotrophs use effectively all the trophic energy available to them. As most or all species overlap with some others in the food they can eat, some or all species use food that others would have used if they were able to do so. This is a kind of competition, whatever may have prevented the losers from getting the energy (cf. Mac Arthur, 1972).

We can define competition generally as occurring whenever at least two individuals or other entities interact so that at least one is adversely affected (37), and any net advantage to any winner is no greater than would have occurred if the loser had been absent initially.

The second proof of the ubiquity of competition is more restricted, although applicable to all communities, and applies to sets of species which are trophically similar and so could share a common ultimately regulatory factor. Such a factor (Lack, 1954; Van Valen, 1973c) is what controls the average density (more precisely, average energy use) of a population over ecologically long intervals. To simplify the argument, which would otherwise need two stages, I will consider energy use over a broad region such as a biogeographic province. This eliminates the need to consider local extinctions, because all species persist regionally. For the soil microbiota an equally heterogeneous region may perhaps be a square meter. Mean population density can be substituted for energy use but its control incorporates subordinate strategies, such as for body size, and so diffuses the picture.

Clams are sometimes thought to be relatively noncompetitive (Stanley, 1974). To make the argument concrete, we can think of it as applying to the sublittoral Pelecypoda of muddy and sandy bottoms in the Montereyan Province on the California coast. Any other unified set of organisms will do (38).

As Darwin noted, all species have a tendency to increase multiplicatively. More precisely, their trophic rates of increase (r_t) of energy use are positive. The actual rate of increase (r_a of Van Valen, 1973c) of almost any species is effectively 0 over ecologically long intervals, because the species persists regionally and doesn't expand indefinitely. Moreover, every species has negative biotic effects on it (predation, if nothing else). If so, r_t is necessarily positive for each species.

The existence of a positive r_t, together with the indefinite persistence of a species, entails that there be a regulation of the species that depends on the amount of energy use. This is simply a rephrasing of the standard conditions for density-dependent regulation in a finite world. Those ecologists who believe density-dependent regulation is unimportant or even inapplicable to natural systems (e.g. Andrewartha and Birch, 1954; Ehrlich and Birch, 1967; Reddingius, 1971; Spight, 1974) also believe (as they must) that extinction is prevalent at the level they consider.

What determines the number of species of clams (or, equivalently, what ultimately regulates each species) is unknown. For the present purpose this doesn't matter. All real possibilities seem to be included under the categories of (1) physical stresses, (2) use of space, (3) predation (including parasitism), (4) nutrients, and (5) chemical or other interference. I take it as obvious that ultimate regulation by space, nutrients, and interference will involve competition in any habitat which more than a very few species can tolerate, and I will therefore consider the other two cases (cf. Mac Arthur, 1972).

If predation is ultimately regulatory for a species, each individual (or each unit of energy use) has a higher probability of predation at high density than at low, whether or not there is a threshold in this density effect. Such a change in susceptibility can occur in three ways: (1) by a deterioration of the prey when it is denser; (2) by a search image or equivalent switching pattern by a generalist predator, so that the predator concentrates disproportionately on denser prey species; or (3) by specialist predators increasing when their prey species do, but at a faster rate. High predation with equivalent effects on individuals of all species simply results in the most r-selected species outcompeting the others (Grassle and Sanders, 1973; Van Valen, 1974a) (39). Predation can have major effects on community structure (e.g. Maiorana, 1976) without being density-dependent at all.

Any deterioration of the prey at high density would be caused by some other factor than the predation; this other factor, rather than predation, is then ultimately regulatory. Parasitism, being an aspect of predation, is excluded here as a factor in causing deterioration. For generalist predators, the prey species that is most resistant to predation at high regional density will increase at the expense of the others. This is an aspect of competition (Mac Arthur, 1972), and the more effective competitor gets more trophic energy as a result. With only specialist predators (which could be bacteria, as in Haldane's [1949] original treatment of the mechanism) there need not be competition among the prey. This is because a predator-prey system can be self-regulatory (like the Opuntia-Cactoblastis system) and therefore need not affect other such systems if there is an excess of resources locally. However, such a system can itself be regulated by other mechanisms and this seems to be the usual situation (Van Valen, 1973c).

For physical stresses to be more severe at high density than at low, the individuals must either have lower average resistance at high density or live in poorer areas then. As is the case for predation, the first alternative leads to another factor being ultimately regulatory (or the habitat being competitively partitioned) if coexistence is to be maintained. And the second alternative here is really an aspect of regulation by space: accessible good areas are filled early, when the overall density is lower. Space is a surrogate resource for trophic energy. Physical stresses can permit some species to survive which otherwise could not, but the assumption that they otherwise could not (on a regional basis) is itself an assumption of competition, this being the case for all species that can tolerate more normal habitats.

The stress-competition equilibrium is of just this nature (40). It has two cases. In the first, physical stresses or predation selectively remove

some species locally. In the second case, enough individuals are removed of
the species which is competitively dominant in individual-level competition,
even if the removal is nonselective, that an ultimately regulatory resource
(such as settling space) becomes temporarily available. In each case of the
equilibrium the species best able to use the now abundant resource rapidly are
those that are subordinate in individual competition. Such stress-adapted
species are of two kinds. For the first kind the term resistant species (Van
Valen, 1971a) may be extended. Resistant species can tolerate stresses that
are severe to other species and still survive as individuals. Predation-
resistant species, like heat-resistant species or disturbance-resistant
species (cf. Kranz, 1972), are examples, whatever the mechanism of resistance.
The second kind of species may be called resilient species. They are individ-
ually susceptible to stresses but their populations rapidly recover, or they
easily establish new populations.

   If the stress doesn't recur soon, the good individual-level competitors
can gradually reinvade to form a biotically integrated community in which the
stress-adapted species are competitively subordinate or excluded except by
dispersal from recently stressed areas. The stress-competition equilibrium
depends on sufficiently severe stresses being frequent enough so that individ-
ual-level competition doesn't exclude stress-adapted species, and yet not so
frequent that competitively dominant species are eliminated.

   Jackson (1973) thought that the occurrence of most clam species together
in the physically most favorable subtidal zone is evidence against the
stability-time hypothesis. This would be so only if total competitive ex-
clusion were more rapid than repopulation by larvae from the physically stress-
ful zones. For species just as for genes, there can be a balance between
dispersal and selection, and the same equation holds for both cases. Jackson
(1974) cited the relatively low standing crop of clams in some habitats as
evidence against competition, because the low biomass is maintained there by
predation (41). But competition and predation aren't mutually exclusive. A
predation-resistant species, or a resilient species, can outcompete a com-
petitively dominant but predation-susceptible species in an environment with
enough generalist predators (42). There must be some way in which all the
species of clams are able to coexist, because they do. And all known realistic
mechanisms for their coexistence involve competition. The problem is difficult
(Dayton and Hessler, 1972; Grassle and Sanders, 1973), but an answer to it is
equivalent to an answer to the nature and mechanisms of competition.

   That the stress-competition equilibrium seems to fit clams as well as
other organisms is presumptive evidence that competition is, at some level,
important. Levinton and Bambach (1975) and others have given evidence for com-
petition by clams for food itself, and Jumars (1975) and others have shown that
even in the deep sea there is appreciable environmental heterogeneity on a
local scale. The possible exception to competition provided by specialist
predators does not, for these reasons, seem to control the structure of clam
communities.

DIMENSIONS OF COMPETITION

   In the rest of the paper I develop a theory of competition based on energy.
The development is based on species as the competitors, but other phenotypes
or taxa, or even alleles, can often be substituted. I then apply aspects of
the theory to species diversity in the deep sea and to differences in the
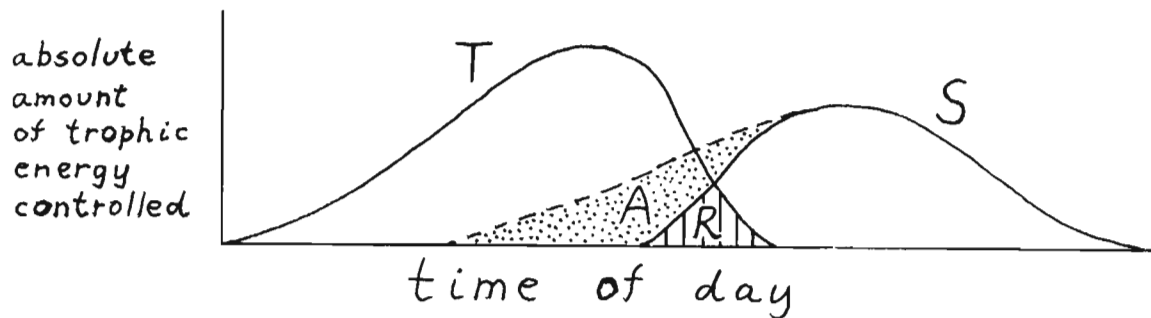evolution of clams and mammals.

Figure 1. Effect of competition of species T on species S, both being
insectivores. The solid curves represent each species' actual control of
energy obtained at each time of day and the dashed curve represents the addi-
tional control S would have without T. R (as a proportion of the area under
the solid curve of S) is the overlap of T on S, and A (as a proportion of the
area under the total curve of S) is the amount of competition of T on S. The
ratio of the areas A to R is the competitive pressure of T on S. There is no
assumption about the distribution of total energy along the horizontal axis,
which represents a surrogate variable that partly determines what kind of prey
is available to insectivores.

     *   *   *

Amount and pressure of competition

Two aspects of resource competition are commonly confused. These can be
called the <u>pressure</u> and the <u>amount</u> of competition. A resource must be in
short supply at least relative to the capabilities of the species before there
can be competition for it, i.e. the resource must be scarce enough to have a
depressive effect on one or more demographic parameters or on expansion. And
competitive exclusion can occur only with respect to a resource that ultimately
regulates at least the excluded species (cf. Van Valen, 1973c).

Consider a resource (43) in at least relative short supply for some species
S, and some other species T whose resource use partly overlaps that of species
S (Fig. 1). Draw a curve (or, for discrete resources such as food species
whenever the species themselves are relevant, draw bar graphs) representing
the amount of the resource that species S controls of each size or kind. If
the resource is total food and is measured by energy, the area under the curve
is the realized dominance of S. Then the realized <u>resource</u> <u>overlap</u> R of T
on S is the proportion of the area under this curve which T also uses (44).
The competition may be by efficiency or interference. The dotted area in
Fig. 1 represents the additional amount of resources that S would control if
T were absent (45), and so when added to the realized dominance it gives the
potential dominance of S conditional on the absence of T. The extension
beyond one dimension of surrogate resources is obvious, the only new feature
being possible interaction among resources.

The <u>amount</u> A of resource competition of T on S is the total effect of T
on S in reducing the resource control of S:

$$A = \frac{e_p - e_a}{e_p} ,$$

(5)

where e_p is the potential amount of the resource that S would control in the
absence of T and e_a is the actual amount it does control when T is present.
The amount of competition of T on S may differ from that of S on T; the compe-
tition may even be unidirectional (46).
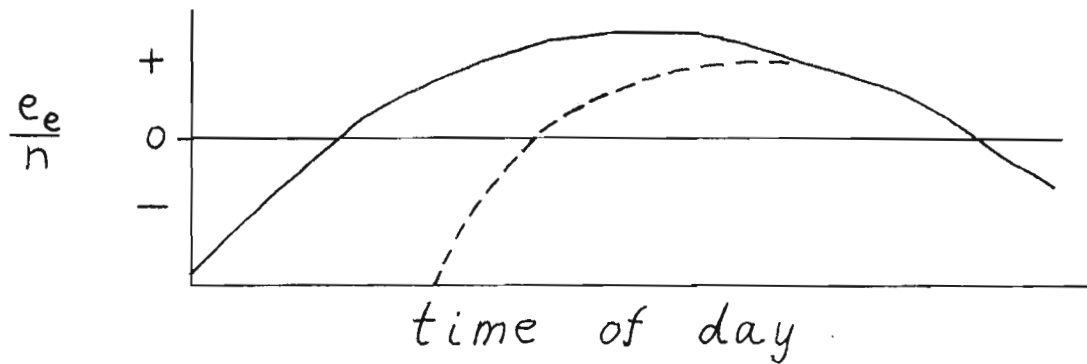
$$\frac{e_e}{n}$$

time of day

Fig. 2. Favorable and unfavorable regions for an average individual in a population of insectivores without (solid curve) and with (dashed curve) competition. e_e/n is mean expansive energy (total energy intake minus maintenance and waste energy) gained per individual active at a given time of day. The height above the horizontal line at 0 (the line of expansive sufficiency) represents energy available for growth and reproduction; the region where the curve is below the line must be subsidized energetically by the favorable region above the line.

*   *   *

The competitive <u>pressure</u> P is the effect of T on S per unit overlap: in Fig. 1, it is the ratio of the dotted area to the lined area. It is related to the realized overlap and amount of competition as follows:

$$P = \frac{A}{R(1 - A)},\tag{6}$$

whence pressure increases hyperbolically with amount if overlap is constant (47). Alternatively, $A = PR/(1 + PR)$, and $PR = (e_p - e_a)/e_a$.

The intensity of competition is often measured by the overlap in use of a resource or in a surrogate variable such as temperature, but overlap in itself has no effect on either individuals or populations. Its apparent effect comes from its relation to pressure and amount. I expect that the realized amount of competition between ecologically adjacent species, near equilibrium, is the most constant of the three parameters (48). If so, near equilibrium the overlap is negatively related to the pressure of competition. Overlap is expected to be positively related to amount, because the referent species is now prevented from using at least much of the resource that is overlapped as well as perhaps more (49).

The force of competition from other species selects for reduced overlap and a lower amount of competition. But there is an opposite force: the tendency of populations to expand their adaptive zone as much as possible. The equilibrium between these forces determines the amount of competition and the realized overlap. At equilibrium the compressive and expansive forces are necessarily equal at some point.

The force compressing the realized adaptive zone acts on individuals by the competitive pressure, but its effect on the population is measured by the amount of competition. This is a main reason for introducing the concepts.

An individual suffers from resource competition only when it uses resources in the zone of overlap, and how much it suffers is, on the average, directly related to the amount of its own species' potential resources that are appropriated by the competitor. When this appropriation is much larger than the overlap, any individual affected at all will be affected more than when the
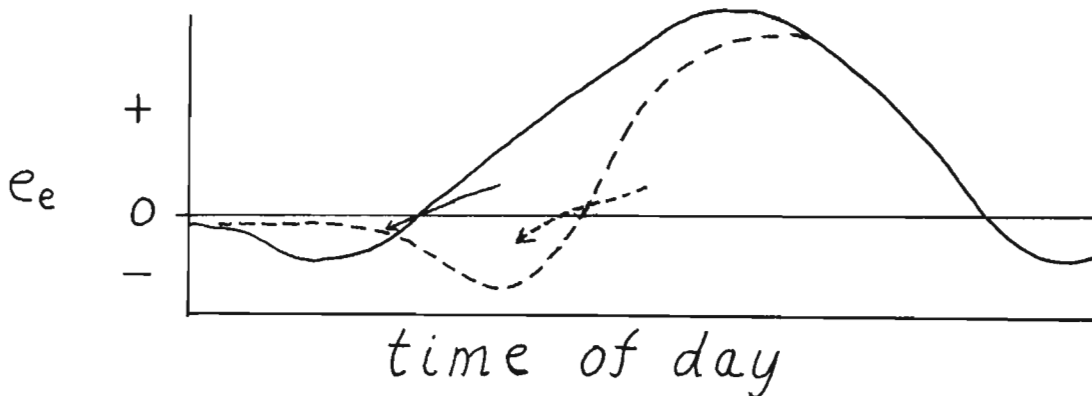
Fig. 3. Amount of expansive energy gained by the entire population of
insectivores without (solid curve) and with (dashed curve) competition. The
arrows indicate the directions of movement of energy that subsidizes unfavor-
able parts of the adaptive zone.

       *   *   *

appropriation nearly equals the overlap. What happens to the individual may
be the same in each case, but in the second case the detriment is caused
partly by the individual's inherent inability to use more extreme resources.
Thus competition has a greater effect on the individual when competitive
pressure is greater and therefore is more important in individual selection.
At the population level, on the other hand, it is simply the amount of compe-
tition which measures the loss of resources and so the effect of competition.

Expansive sufficiency

    Consider the relation between energy use and position on a resource axis
(Fig. 2). At equilibrium there must be some region where the average energy
intake per individual is greater than the sum of the energy used for main-
tenance (including food-getting, predator defense, etc.) and that wasted,
including wastage by death, because individuals must grow and reproduce. This
region I call the favorable region of the adaptive space. On some resource
axes (as well as on axes like that for temperature) the effect of the resource
position on the mean total energy intake eventually causes the latter to fall
below the maintenance and waste energy. This decline may be due to mortality
as well as lower efficiency. If an individual is weighted by its energy use,
the height of the curve is proportional to the product of the food-gathering
efficiency and the instantaneous probability density of survival.
    The exponential population growth sometimes permitted by the favorable
region subsidizes the unfavorable region. Individuals disperse into the un-
favorable region, or spend some time there actively, or eat some of the food
it represents: whatever resource the axis signifies. Some individuals may
grow and reproduce in the unfavorable region; in that case more individuals
lose net energy there. The curve is merely an average. Most individuals
(units of energy use) will ordinarily be in the favorable region; therefore
the curve for expansive energy gain by the population (Fig. 3) differs from
that for individuals. There is proportionally less loss in the unfavorable
region because fewer individuals are there at any one time.
    The height (s) of the line of expansive sufficiency for an individual of
size n is

$$s = \frac{e_m + e_w}{n} .$$

(7)

Above this line energy is available for expansion. All the energy except the metabolically oxidized part of e_m is available for other species if they can get it. The region where $e_e > 0$ for an average individual is the favorable region; unfavorable regions are where the mean $e_e < 0$, including the effects of higher mortality. The line of expansive sufficiency can for most purposes be expressed as a constant although it does depend on some variables, such as temperature even for homeotherms (50).

I conjecture that for all regionally coexisting species, or in general for all self-perpetuating phenotypes, there is no overlap in their realized favorable regions of the adaptive space when all relevant axes or variables are considered, except as specifically noted. The variables must include at least (1) whatever limits the micro- and macrogeographic boundaries of the ranges of the species and (2) the factor or factor interaction that ultimately regulates density in each part of those ranges (51).

The proof is simple in outline, although bounding its domain is harder. An ultimately regulatory factor of population density is one that reduces the difference between the expansive energy of the population, and its losses to death, attrition, and the like, to zero and below as density increases or as the factor increases in intensity (52). Assume two populations with overlapping favorable regions in the adaptive space, and measure their densities in units of energy control. By the axion of inequality (Hardin, 1960) the densities differ at which the two populations lose all their expansive energy. These densities sometimes occur. At just above the lower of these two densities one population declines and the other continues to increase. Thus only the latter maintains a favorable region in this part of the adaptive space (53).

The domain of truth of the conjecture excludes some situations, by no means all, of frequency-dependent predation, frequency-dependent interference, and of an abundant species excluding another from part of the unfavorable region of the first species (54). Other limits to the domain may possibly occur. The domain of the conjecture above seems broad, however, and whatever its domain it may be the most general form possible of the principle of competitive exclusion.

Competition can of course occur for resources that aren't ultimately regulatory. In this case both or all phenotypes may each increase their energy control, but the rate of increase is likely to be affected. Despite the views of Hulburt and Horton (1973) and others, this situation is irrelevant to competitive exclusion. It is irrelevant simply because it gives no means by which exclusion will occur. If exclusion (or even contraction of the adaptive zone) does occur because of such competition, this in itself shows that the resource was then ultimately regulatory for the loser in that part of the adaptive space (55).

With respect to resources which aren't ultimately regulatory, or for other environmental stresses, there is no barrier whatever to convergence (56). Cody (1973, 1974) and others have in fact thought, at the other extreme, that convergence automatically happens when species are more similar than a threshold value and that convergence is accentuated by a shortage of resources. This too fails to consider how the species are ultimately regulated and therefore how they coexist (57).

Competition reduces the population's expansive energy. But if the population is to survive, it must maintain some expansive energy. The curve of Fig. 3 indicates the net movement of energy from the favorable region into the implied zone of overlap. Expansive energy is dissipated by (1) density-dependent regulation, (2) subsidy of unfavorable areas, and (3) dispersal. These mechanisms are not mutually exclusive. The compressive force is the expansive force for one or more other species (58). If the species are to coexist

regionally, there must be some set of variables (not restricted to resources
and including such things as the lag period before exploitation of a newly
available resource, and variation as well as average values) where each species
has a favorable region that is unfavorable for the others in the presence of
the first species. Therefore the equilibrium is determined by the shapes of
their curves of expansive energy, in particular by the points where these
curves cross each other and cross the line of expansive sufficiency of its own
species. The latter can be called the critical point or line. The fact that
the lines of expansive sufficiency are of different heights for different
species is an important aspect of competition (59).

Coexistence and the force of expansion

The force (60) of expansion E of a species (or other self-perpetuating pheno-
type) is the rate of flow of energy from its favorable region. This flow is
defined at any point in the adaptive space and measures the resistance of the
species to encroachment by competitors at that point, as well as measuring the
species' effectiveness in its encroachment on others there. It is itself
measured in units of trophic energy control, because this is what affects
other species. It too can be partitioned in various ways. At any point or
interval i in the adaptive space, where there are n_i energetically equivalent
individuals at a particular time,

$$E_{ij} = n_i e_{bij} \tag{8}$$

or

$$E_{ij} = C_{ij} [e_e P(m_i) - n_i d_i + n_i s + e_{ri}]. \tag{9}$$

The value of E_{ij} depends on which species j are competing with the referent
species; the force has the same meaning even if there are no competing species.
$P(m_i)$ is the mean probability per unit time that a unit of expansive energy
moves to i, or the net movement if there is flow from i too. d_i is the mean
individual deficit in expansive energy per unit time at i, or the distance
below the line of expansive sufficiency. The first two terms of the expression
inside the brackets are therefore the expected expansive energy available at
i per unit time. When i is in the favorable region, the terms inside the
brackets need minor verbal reinterpretation to give this result. The function
C_{ij} is the mean competitive ability per individual (or unit of energy consump-
tion). It can itself be partitioned. It can be defined almost conventionally as

$$C_{ij} = \frac{e_{bij}}{e_{ci}} \tag{10}$$

where e_{bij} is the expected amount of energy that one individual controls per
unit time when at i together with equal numbers (x) of individuals (or the
equivalent in energy consumption) of each of the y competing species, including
its own species, and e_{ci} is the expected amount of control when together with
$xy = n_i$ individuals of its own species. Interference effects are included,
and social effects require a minor verbal change. If there are no competing
species, C = 1 for all i. Thus the presence of a force of expansion doesn't
depend on the presence of any competitors. C depends on various subsidiary
parameters such as the proportion of conspecifics in the interspecific situa-
tion, the total number of individuals, their age structure, and the like, but
it is customary to consider it a constant at first approximation with respect
to such variables. Contrary to much theory it does, however, vary importantly
with respect to position on the resource axis, the other species considered,
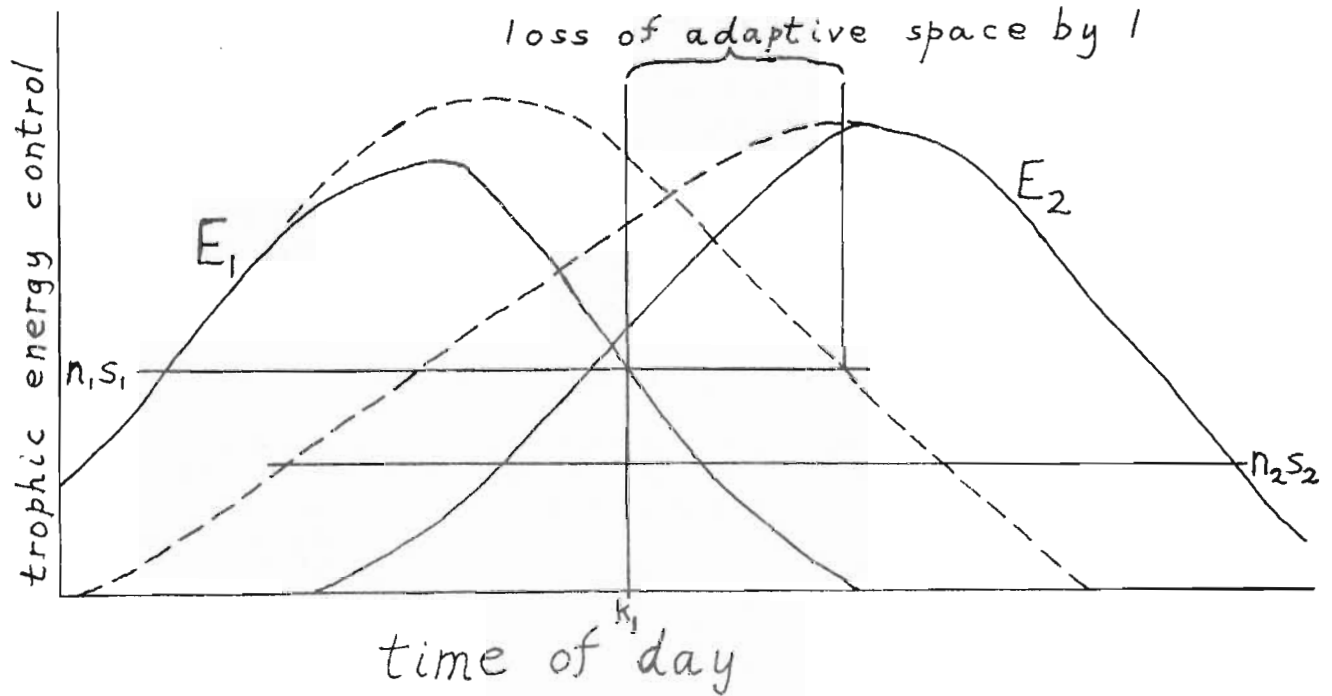
Fig. 4. The favorable regions of two competing species of insectivores, not
yet at equilibrium. ns denotes in a too simplified way the respective lines
of expansive sufficiency and E denotes the forces of expansion. The dashed
lines denote the amount of energy control each species would have if by itself.

    *   *   *

and other environmental influences, and this variation determines much of the
structure of the community.

    A large force of expansion, and the resulting success in competition, is
therefore determined in part by individual competitive ability and in part
by the number of individuals (or other measure of energy use) in the zone of
overlap (61, 62). The other species may, rather than competing, benefit
the referent species by making more energy available, often but not always at
the expense of the rest of the community. In such cases of mutualism and
commensalism $C_{ij} > 1$. Predation can have a formally similar treatment; the
competition coefficient or function is really a more general interaction
coefficient. It is useful to treat predation as a special form of competition
by predator and prey for the available trophic energy.

    The boundary of the favorable regions of two competing species or other
phenotypes 1 and 2 will be determined by their forces of expansion, their
lines of expansive sufficiency, and the amount of trophic energy e available
to them per unit time (Fig. 4). Because for all i $E_{1i} + E_{2i} = e_i$ and for the
critical point $E_{1i} = n_{1i}s_1$, the boundary for species 1 will be a point or line
k such that

$$e_k - E_{2k} = n_{1k}s_1, \tag{11}$$

so that

$$n_{1k} = \frac{e_k - E_{2k}}{s_1}. \tag{12}$$

    The total force of expansion E_j with respect to a particular competitor j
is obtained by integrating E_{ij} over the zone of overlap, because this is the
only region where direct interaction occurs (63). A plot of E_j against the
amount of competition should show a maximum value after part of the potential

favorable region has been lost. Greater encroachment makes the species less able to subsidize its unfavorable region even though the latter is larger.

The amount of its favorable region lost by species 1 as a result of the presence of species 2 is determined by the intersection of the line of expansive sufficiency with the dashed curve of Fig. 4. The dashed curve is the same as E_1/C_1. Competitive exclusion occurs when the expansive energy in the remaining favorable region falls below some minimum amount that depends on the species and environmental fluctuation. The favorable regions of the two species may often not adjoin each other because of competition in their unfavorable regions, subsidized by the favorable regions.

Central and marginal selection

Where adaptive zones are sharply bounded by the structure of noncompetitive aspects of the environment, movement into an unfavorable region is likely to have a low probability of success per individual, and so it should be selected against. But where adaptive zones are competitively bounded this is far from the case. Here a force of expansion is necessary for survival. Any species that everywhere has a greater expansive force than its competitors will oust them. But the force of expansion declines away from the optimal part of the favorable region of the species. Except where a species reaches its physiological limits (or limits imposed by predation, if predators are excluded from the class of competitors), the species will expand in adaptive space to its critical point with respect to its present competitors. It will ordinarily expand somewhat beyond this point also.

The movement of energy outward in adaptive space from the favorable region is by individuals, the relevant movement of energy being in part the movement of the potential for these individuals to control energy because maintenance, expansive, and waste energy are measured as rates. The optimal situation, for an individual, stated by Mac Arthur (1972) in a somewhat different form, is for the individual to move in adaptive space if its expected control of energy elsewhere is greater than that where it is now. The time scale of selection is important here, partly because a parent may disperse progeny such as seeds in a way that maximizes their total control (maximean strategy for parent) rather than the control by each progeny individual (maximin strategy for offspring). The time scale for the evolution of present behavior also enters because of environmental variability: the maximum expected control of energy in the immediate future may be at a different place in adaptive space from the maximum probability of successful reproduction later.

The greater the amount of density-dependent mortality (or other density-dependent reduction in fitness) in the favorable region of the adaptive zone of a population, the more advantageous it becomes for an individual to move to the unfavorable region. In the latter region there is less competition, at least with conspecific individuals, but other aspects of the environment are harsher. Variation among individuals in fitness is ordinarily greater in the unfavorable region (64). Ideally movement will be at a rate such that the mean (expected) fitness of individuals at each point in the adaptive zone will be the same (65). Since different components of fitness have different importance away from the favorable region, however, even in a constant or otherwise predictable environment such a distribution may be hard to achieve. This effect is in addition to the presumptive conflicts between adaptations for the favorable and unfavorable regions. The difference between selection in and out of the favorable region is not that between K- and r- selection. Everywhere in adaptive space that the carrying capacity can be increased it
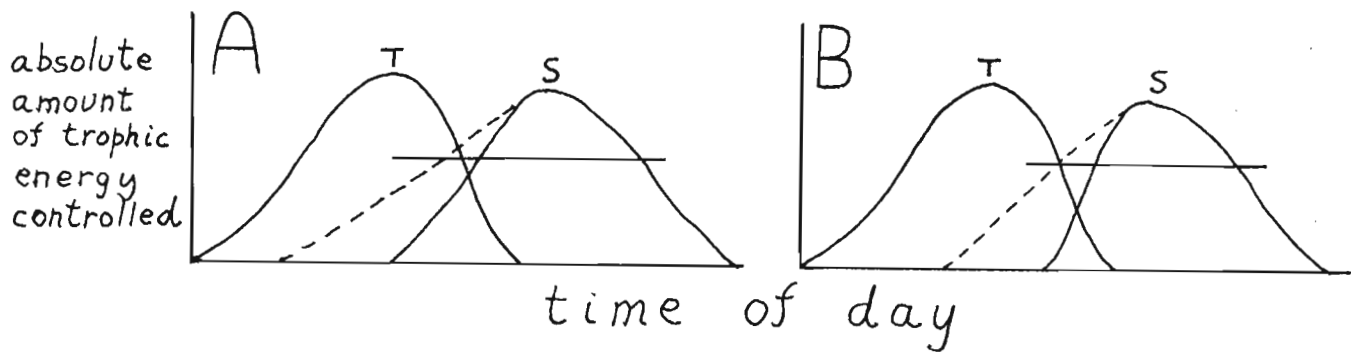
Fig. 5. Realized (———) and immediately potential (-----) resource gain by an insectivore population S just after an unchanging competitor T arrives (A) and at selective equilibrium (B). The horizontal line is the line of expansive sufficiency for S.

       *   *   *

will be, and reproduction and dispersal are also about equally useful at all points. The difference is in mechanisms rather than in relation to density.

The harshness of the unfavorable region may be due to predation, desiccation, poor food relative to a species' needs, encroachment by another species, or much else, and each kind of harshness obviously selects for any appropriate adaptations. A single population may have several kinds of unfavorable regions, overlapping or not. With density of conspecifics the greater problem in the favorable region, interference and efficiency seem the usually available responses. But each kind of selection, which may be called central and marginal (66), occurs in each population and often on each individual. The population would control more energy if it could subdivide itself into locally restricted subpopulations, each dominated by either central or marginal selection. But the movement among regions, necessary because the unfavorable region must be subsidized energetically if only by progeny, acts against this solution and produces individuals whose phenotypes have been shaped by both kinds of selection. Such individuals will be scarcer in the favorable region than in the unfavorable if the movement is sufficiently unidirectional.

Evolution away from competition

When a new species of competitor arrives, it will ordinarily have its greatest effect on and near the now unfavorable region, at least if the two species manage to coexist. It will not increase the expansive force of the original species in other directions unless the surplus expansive energy that produced movement to the region of the new competitor is maintained and successfully diverted (67). If enough expansive energy is lost to the new competitor even the reverse may happen: the species is then unable to subsidize its expansive force in other directions as much as before and therefore contracts its realized adaptive zone in directions additional to that of the new competitor.

The new competitor selects for reduction in overlap by making it less profitable (for both species) for an individual to stay or remain in the zone of overlap (68). Competitive ability in the relevant part of the adaptive space may also, or instead, increase (69). The pressure of competition normally increases (Fig. 5); it does so if and only if the proportional reduction in the absolute amount of overlap (the vertically ruled area in Fig. 1) is greater than the proportional reduction in unrealized potential resource control (the dotted area in Fig. 1). Letting overlap and unrealized potential resource control be represented by a and b respectively, the proportional

change in pressure is

$$\frac{P_2}{P_1} = \frac{a_2 b_1}{a_1 b_2} .$$

(13)

The amount of competition may increase or decrease.

$$\frac{A_2}{A_1} = \frac{e_{p1} e_{p2} - e_{a2} e_{p1}}{e_{p1} e_{p2} - e_{a1} e_{p2}} ,$$

(14)

so the amount increases if and only if the proportional reduction in the actual control of resources is greater than the proportional reduction in the potential control, the sign of the change being that of ($e_{a1} e_{p2} / e_{a2} e_{p1}$).

The movement of surplus expansive energy toward the competitor is likely to be reduced (compare the fitness distributions in Fig. 2 without and with the competitor), and therefore the force of expansion in that direction decreases at least in the farther part of the original unfavorable region. This selective response to competition can be rapid (Seaton and Antonovics, 1967). The surplus expansive energy saved by this response is then available for diversion elsewhere, if such diversion is possible (70). The diversion is an alternative explanation to facilitation (the inverse of interference) for the greater yield sometimes found, by methods like the diagram of de Wit (1960), in mixtures of phenotypes than is found for either alone (cf. Barker, 1973; Real, 1975). I can, however, think of no real studies which have shown how this selective diversion of a competing species' expansive energy to a different part of the adaptive space really occurred. Presumably it occurs universally for early successional species and the like, for such species are always outcompeted locally if the physical environment lets them survive long enough in one place for this to happen.

Adaptations to the zone of overlap are reduced in importance after the arrival of a competitor because fewer individuals occupy the zone. Therefore developmentally or functionally conflicting adaptations to other parts of the adaptive space may be selected for. Thus a species can sometimes expand its favorable region in a direction away from the new competitor (71).

The potentially favorable region of a population (the favorable region immediately after the competitor vanishes) decreases as selection against overlap proceeds. This produces species with narrow adaptive zones (72). But the process is reversible if the competitor does vanish. Ecological release, the expansion of the favorable region when a competitor disappears, thus has two time scales. The first occurs at once (73), by the occupation of the immediately potentially favorable region. The second time scale is that of evolution to expand further the realized favorable region, creating a progressively more divergent potentially favorable region as a byproduct whenever there remain any competitors more distant in the adaptive space. The force of expansion can be constrained developmentally or functionally as well as competitively, but I have thought of no case (S. Levings thought of aphids, and I agree) where this is important on an ecological time scale rather than an evolutionary one.

High-pressure and low-pressure competition

It is useful to consider the continuum of competitive pressure. On this axis the extremes can be called high-pressure and low-pressure competition.

They have appreciably different effects and occur under different circumstances. Interactions among mammals and clams may be taken respectively as examples of the two types.

High-pressure competition should characterize, as a first approximation, habitats that are both relatively stable and favorable for many species (74). These are the biotically accommodated habitats of Sanders (1968). Overlap is low relative to the amount of competition. Low-pressure competition may characterize two kinds of habitats. One kind is physically unstable and consists of what Sanders (1968) called physically controlled habitats (75). The other kind is relatively stable but physically too extreme for most species. The species that can survive such habitats, such as hot springs, bare rock, or lakes of high salinity, I have called resistant species. Whether the pressure of competition as well as the amount is usually low for resistant species is unknown.

The distinction in habitat types is like that commonly thought to distinguish predominantly r-selected and K-selected communities, and to some extent the correspondence is real. However, Maiorana (1976) has shown that the existence of conflicting adaptations makes the association of r- and K-selection with habitat types a poor one. And the correspondence of r-selection and low-pressure competition is itself imperfect (76). A species adapted for early succession in a generally favorable habitat is extremely r-selected. But because it can survive in such habitats and is excluded from them most of the time, the amount of competition on it is large (77). Such a species is therefore subject to a rather high, and perhaps very high, competitive pressure.

Moreover, as with r- and K-selection, it really isn't habitats per se but regions of the adaptive space that are relevant. Generalists can exist in any habitat, and so can fugitive species. The main result of high-pressure selection at the population level should be a relatively narrow realized adaptive zone. This narrowness is specifically in the parameters that ultimately regulate the densities and limit the distributions of the species and its competitors. Any other parameter can of course vary freely, without this kind of constraint (as Preston [1973] found without realizing it), and there is no obvious reason to expect a difference in such dimensions as a result of competitive pressure. Grime (1974; Grime and Hunt, 1975) has in fact found that forbs which are early colonizers seem to have relatively narrow adaptive zones when appropriately examined.

Low-pressure selection and competition affect more individuals than do their high-pressure counterparts, but the effect on the average individual in the zone of overlap is correspondingly less severe. The cumulative effect, the amount of competition, can be the same, and it is this that determines many adaptations. The non-interactive equilibrium of Simberloff (1969) and Wilson (1969) is an extreme case of low-pressure competition, so low that competition vanishes. Such an equilibrium may occasionally occur briefly and on a local scale in very unstable habitats (78), but because colonizing ability is itself an aspect of regional competition it is forbidden on a regional level. Here too the minimum size that we can take for a region depends on the distance over which colonization takes place.

In high-pressure and low-pressure communities different proportions of trophic energy are used for adaptations to the physical environment and to other species. Such adaptations are highly varied; for physical stresses they include adaptations as diverse as those for burrowing ability, diapause, dispersal, heat resistance, and structural strength. A species which uses much of its trophic energy and developmental pathways in such adaptations has less left to deal with predation and competition. At the level of individuals,

this is where the two kinds of selection exert their divergent effects most
importantly. Of course some species in a community are more affected by the
physical environment than are others. This often leads to a mingling of high-
pressure and low-pressure species in the same community, although not in the
adaptive space.

The distinction between dominant and regulatory influences on population
density (Van Valen and Sloan, 1966, under a different name; Van Valen, 1973c)
is somewhat similar to that based on competition. In the present context,
dominant factors are those that cause most of the reduction of the mean ex-
pansive energy per individual in a population below what it would be at optimal
density and without competitors or predators. Direct factors (Patten, 1975)
are all such influences irrespective of strength. Those direct factors that
are also regulatory are likely to be related to competition, but any direct
factor whatever is a selective vector in proportion to its strength (Van Valen,
1973c). However, a species can be regulated in different ways in different
places. Some local regulatory factors (such as a species-specific predator)
conceivably need not be related to any zone of overlap in the full adaptive
space, although any ultimately regulatory factor that does operate in such a
zone of overlap is an aspect of the competition.

Factors that affect competitive pressure can have recondite effects.
Physical fluctuations in the upper ocean have different effects on different
parts of the marine benthos. Levinton (1974) has noted that the food of
suspension-feeding marine benthos varies more over time than that of deposit-
feeders. He concluded that the trophically more stable environment of
deposit-feeders lets them be more conservative in their evolution. The fluc-
tuation in the suspended plankton, corpses, and fecal pellets, though, is
itself related to physical fluctuations nearer the surface of the ocean. The
entire marine benthos below the euphotic zone is trophically restricted to the
decomposer system, as even living phytoplankton there have sunk beyond hope
of longer life. But this system is heterogeneously related to its food supply
and so is differentially affected by distant physical stresses.

The effect of predation on competitive pressure is ambiguous at the present
level of theory. Predation normally results in reduced expansive energy for
the prey. The favorable region is therefore less able to subsidize the
unfavorable regions. This should result in a contraction of the occupied
unfavorable region and less overlap with other species. But other prey
species are similarly affected. Therefore the amount of competition also
declines. (This decline in the amount of competition among the prey is more
or less balanced by the energy going to the predators.) The direction of any
change in competitive pressure then depends on whether the amount of competi-
tion or the overlap declines more. If predation affects one prey species
more than another, the pressure of competition on the first species increases
and that on the second species decreases. The decline in the expansive force
of a competitor may lessen the reduction in overlap or even lead to an increase
in overlap. Thus a decrease in pressure may be a more common result of preda-
tion than an increase. Predation can also increase or decrease the number of
species of prey (Harper, 1969; Van Valen, 1974a). Therefore, by adding or
subtracting entire favorable regions, it directly changes both the amount of
competition and the amount of overlap. Again the direction of predominant
change in pressure is ambiguous, this being so whether the number of species
increases or decreases.

For a given number of dimensions of ultimately regulating factors of
density, a higher number of coexisting species ordinarily requires that the
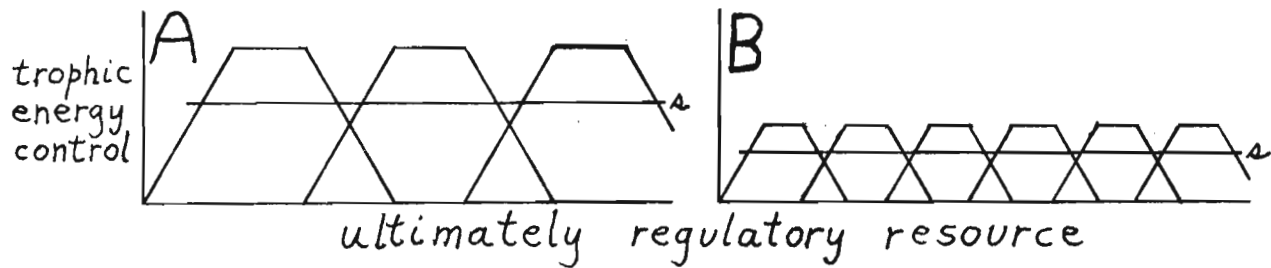
Fig. 6. Diagram to show how more species can fit into a habitat with the same values of the parameters of competition when their lines of expansive sufficiency (s) are lower and the habitat has proportionately less trophic energy. The species curves can be any shape as long as the shapes are the same in the two cases.

*   *   *

mean overlap on these dimensions be lower. This is simply because almost any new species must locate its favorable region in a previous zone of overlap, unless there were regions of unused trophic energy. This reduces the energy available to the species previously overlapping there and should therefore reduce the amount of the adaptive space they occupy. The fitness functions in the regulatory dimensions are steeper (Fig. 2), so the mean overlap should be less.

The deep sea

One would therefore think that the floor of the deep sea, with its high diversity of species, must be a habitat of high competitive pressure. But this may not be correct. If the lines of expansive sufficiency are lower in a community of more species, more species can easily fit with the same pattern of competition (Fig. 6). This would be possible only if the amount of trophic energy available is proportionately lower also (79). The metabolism and growth of at least some deep-sea organisms are known to be remarkably low (Jannasch and Wirsen, 1973; Smith and Hessler, 1974; Turekian et al., 1975; but see Seki, Wada, Kioke, and Hattori, 1974), although this doesn't yet seem to have been quantitatively compared to the low rate of fall of organic detritus. Such a comparision would set some bounds on the competitive structure of the deep-sea biota, as would in a different way a comparison with the rate of accumulation of reduced carbon below the bioturbated zone in the sediments. A measurement of the total metabolism of all sedentary organisms in some small deep-sea samples has been made (Smith and Teal, 1973) and its proportional decrease below the values for shallow-water samples is comparable to that of metabolic rates. This is as yet the best information on the total availability of trophic energy to the deep sea floor, because (as elsewhere) little remains unused (80).

This hypothesis that low energy availability, and metabolic adaptations to it, can itself lead to an increased diversity of species is the reverse of the usually assumed positive relationship between diversity and energy availability. If there were no change in the lines of expansive sufficiency it is indeed true that fewer species would fit the same competitive pattern if there were less energy (81). There is a formally similar association of high aquatic productivity, normally in polluted waters, being associated with low species diversity. But this seems to have a different mechanism: a species

adapted to a zone in adaptive space where energy is now concentrated subsidizes its unfavorable regions so strongly that its expansive force is greater there than that of other species whose favorable regions are in this subsidized area (82). If the floor of the deep sea really is less variable than most other habitats, when measured on the greatly slowed time scale of its inhabitants, the commonly cited influence of a relatively constant environment or species diversity would supplement that of low energy availability.

CLAMS AND MAMMALS

Stanley (1975) has said that "the set of characters that we see today [among clams] is the result of relatively weak selective pressures acting separately upon individual lines of deseent." This supposed unimportance of competition among clams thus affects our interpretation of much of the evolution of this group and, by extension, of many other groups.

If there is a major difference between clams and mammals in the importance of competition, a variety of apparently unrelated differences between the groups are explained. This is why Stanley's approach seems persuasive. But I argued in a preceding section that low-pressure competition can easily occur together with a large amount of competition. And I argued earlier that competition is in fact important for clams. Here I present each of Stanley's arguments (1974, 1975) for there being little competition among clams, relative to that among mammals, and comment on each from the standpoint of theory in the present paper.

(1) Archaic groups of clams persist without being confined to geographic refugia. Comment: The survival of primitive clams implies that they do what they do better than groups that are advanced in more characters, so any general adaptations (83) of the latter groups don't more than offset the specific adaptations of the more primitive groups. The existence of general adaptations is the reason for the common mistake of equating primitive characters with adaptively poor ones. Which state was primitive is entirely irrelevant for special adaptations unless there is structural or developmental irreversibility. General adaptations may well be more prevalent in the evolution of mammals than in that of clams. If so, this is presumably due to something like the greater complexity of mammalian structure and behavior rather than to a difference in competition. Greater complexity gives a greater possibility for novelty because more things can be modified. And occasionally novelties may be of general use. Also, the difference of clams from mammals may be small. Monotremes have persisted (if weakly) in the face of a large marsupial radiation in Australia, and almost as many South American genera invaded North America as the reverse after the Pliocene land bridge was completed (Patterson and Pascual, 1972).

(2) Many clams have reversed their evolution to get primitive body plans and habits. Comment: There are few enough characters involved for them to do this easily. That they do so implies an often-occurring selective advantage for the primitive states; in the real world there is no important selection without competition, except for adaptation to intolerable changes in the physical environment, although this competition can be within species. Loss of an adaptation is well known to occur when it interferes with another adaptation that is now more important. The frequency of occurrence of general adaptations is relevant here too. Convergence of coexisting species is forbidden only for characters involved in the ultimate regulation of a species'

density or in species recognition. Anything else can converge freely, and
this happens commonly for mammals as well as clams (e.g. high-crowned teeth
in grasslands, size change on islands, pelage color on snow).

(3) More than half the families of the Pelecypoda are still alive, and
an increase in number of families and genera has continued throughout the
Phanerozoic. Mammals arrived at an equilibrium in the early Cenozoic.
Comment: The increase for clams is perhaps spurious (cf. Raup, 1972). If
real, it is unclear to what extent the increase is within habitats and to
what extent it is from a decrease in the average number of habitats occupied
by one species, or even from an average increase in the total number of
habitats occupied by the class. If clams have increased their average compe-
titive pressure over time, an increase in species number would be expected.
Without such basic data, and some detailed knowledge as to how newcomers fit
into the previously existing ecological patterns if there is an increase,
nothing useful can be said except that available data are consistent with
competitive control. Clams have largely replaced brachiopods since the
Paleozoic, perhaps by being more resistant to predation. But brachiopods did
evolve predator-resistant groups in the Paleozoic, so their failure to do so
later implies that their expansion was prevented. Presumably clams have
prevented this expansion. If so, competition is important in the success of
clams.

(4) Mammals evolve much faster than clams, the mean longevity of a mam-
malian genus being about that for a clam species. Comment: The difference
is true for taxonomic turnover but not for the rate of evolution of individual
characters (Van Valen, 1974b). Why mammalian taxa replace each other so
often is unknown. One might expect, for instance, high-pressure competition
to be less stable (result in more extinctions) than low-pressure competition,
but birds, also a high-pressure group, have evolved slowly after their
initial radiation. The slow rate for birds is, incidentally, strong evidence
against the hypothesis (Schopf, Raup, Gould, and Simberloff, 1975) that
measured taxonomic evolutionary rates are an artifact of the degree of com-
plexity of the organisms involved.

(5) Suspension-feeding clams usually occur in clumps rather than singly.
Comment: Herds of mammals have also been reported. For most organisms
there are both advantages and disadvantages to aggregation.

(6) Predation, not food or space, ordinarily regulates clam populations.
Comment: Other workers (e.g. Grassle and Sanders, 1973; Levinton and Bambach,
1975) disagree. Besides, diversion of energy by one species into protection
or escape, so that the species controls more energy, is a form of competition
whenever another species is adversely affected, as by greater predation.

(7) Apparent cases of competition among clams are only superficially so.
Comment: Not at all. Species of Mytilus compete for space by diverse
adaptations to the physical environment, but this is still competition, as
the author of this work, Harger (1972a, b), emphasized. The difference in
burial depths of coexisting lucinid species, the other case Stanely mentioned,
may well be related to escape from different predators, or even be a fugitive-
species situation related to ease of escape from heavy sedimentation (cf.
Kranz, 1972), rather than being accidental as he claimed.

(8) Many similar species of clams often occur together. Comment: Again,
this is irrelevant if the observed similarity is not in what regulates the
species' density. But the large overlap that characterizes low-pressure com-
petition is probably also involved. This is entirely compatible with a large
amount of competition.

(9) There are many more sib species among molluscs than among vertebrates. Comment: As for points 2 and 8.

(10) Character displacement is unknown for suspension-feeding clams. Comment: It wouldn't be expected if low-pressure competition is prevalent, as long as broad overlap is in fact maintained.

(11) The geographic ranges of congeneric species of mammals often abut with almost no overlap, while this situation is almost absent among clams. Comment: Low-pressure competition again predicts this result.

(12) Convergence often occurs among sympatric taxa of clams, unlike the situation for mammals. Comment: As for point 2. Sympatric convergence is common for mammals and the relative simplicity of clams makes it even easier for them.

(13) The adaptive zones of higher taxa of clams are indistinct, unlike those of mammals. Comment: Some mammalian taxa have indistinguishable adaptive zones (e.g. Artiodactyla and Perissodactyla). In each case investigated, however, the similarities are convergent, being related to similar changes from ancestral taxa (Van Valen, 1971b). The distinguishing characters of the taxa are related to an adaptive shift from their ancestors, not necessarily from each other. Higher taxa can coexist in one adaptive zone, even with subtaxa intermingled, if the subtaxa are good enough in their own subzones to repel invaders (Van Valen and Sloan, 1966). Perhaps the characters of higher taxa of clams also arose as a result of adaptive shifts, the overlap coming later by individual subtaxa each undergoing its own adaptive shift. Any general adaptations of one taxon might permit part of it to invade part of the zone of a taxon without such general adaptations. The comment on point 2 is again relevant also. The intermingling of adaptive zones is favored by structural simplicity.

(14) Rudists, reef-forming clams of the late Cretaceous, were more competitive than other clams and had a higher rate of taxonomic turnover. Comment: Possibly rudists, with their adaptation to rapid individual growth, were undergoing an adaptive radiation in a part of the resource space removed from that of other clams. They don't look much like clams, and rate of evolution is presumably determined more by ecology than by ancestry. Competition in reefs seems to be at a higher pressure than on the sea floor, but the relation of this to taxonomic turnover is obscure (point 4) (84).

(15) When faunas of clams merge, as by the opening of a canal, the number of species in each fauna may increase. Comment: With the discovery of diffuse competition we can now see that it is often easier to fit a species into a quasi-gap in the adaptive space than it is to replace an existing species. The quasi-gap may consist mostly of unfavorable regions of several adjacent species or it may be mostly marginal parts of the favorable regions of several species. An existing species may disappear, but if so it need not always even be an adaptively adjacent species (85). There seem to be no comparisons of total faunal abundance before and after faunal merging. Low-pressure competition lends itself more easily to this general process than does high-pressure competition because it produces lower gradients of energy control through the adaptive space, and therefore the favorable regions of adaptively adjacent species are likely to be less sharply bounded and perhaps farther apart.

Some of the above comments are necessarily hypothetical because we don't know, observationally or experimentally, the nature of the ultimate regulation of the densities of clams. This is perhaps the most important single datum in the ecology of any species or other phenotype, although it is hard to

determine and often is easier for sets of species jointly. From it one can
determine how such phenotypes can or can't coexist regionally. This then shows
how competition does or doesn't act. Stanley entirely fails to consider these
two causal and conceptually basic steps. His argument is entirely hypothetico-
deductive, going from a hypothesis to predictions. But predictions can be
true for reasons other than one's hypothesis (86). Any causal chain can be
mapped onto a deduction. A deductively derived conclusion is as strong as
one's assumptions and, because the assumptions are based on evidence, the
probability of truth of the conclusion can in principle be estimated. One can
thereby justify a conclusion independently of predictions, which can then be
made just as if the hypothesis weren't also a conclusion. Darwin did this, but
his method has been forgotten (87).

Clams compete, and perhaps have as much competition as mammals, but their
competition at low pressure has results that make it seem that they hardly
interact at all. The sum of many weak interactions can equal the sum of a
few strong ones, and this can be important in evolution.

The effect of one species on another changes along a resource axis when-
ever the species are adapted to different parts of that axis. The competitive
pressure P therefore measures the effective difference in adaptations. Low-
pressure species such as clams are thus adaptively more similar to each other
than are mammals, perhaps in part because they are simpler.

REGULATORY ENERGY AND THE RED QUEEN

It is now possible to improve the discussion of fitness in an earlier
section by looking more closely at expansive energy.

If Fig. 5, we would like to say that population S is more fit at time B
than at time A even though it controls less energy. We want to say this
because it spends less energy on subsidizing an unnecessarily large unfavor-
able region and therefore has more expansive energy available to deal with
other situations. Natural selection does produce this result, acting at the
level of individuals, and the average individual in the whole population at
B does control more energy than at A.

The increased expansive energy at B is either used to increase the force
of expansion in other directions or serves as additional density-dependent
loss in the favorable region itself. But how to make this precise? We can't
use the mean expansive energy (or mean total energy) per individual as a
criterion, for this changes with density. The total expansive energy may
well have decreased a little from A to B and is therefore also unsuitable.
However, the amount of expansive energy that is expended within the favorable
region has increased, so this is a possible measure. It may be called the
regulatory energy. More precisely, it is the energy that is used in the
density-dependent regulation of the population, including that exported from
the favorable region. For fugitive species and the like, to the extent that
their regulation is on a regional basis the relevant population is of course
that of the whole region. The amount of regulatory energy is, if I interpret
Wallace (1968) correctly, what determines the possible amount of his soft
selection.

For individuals fitness can be treated similarly, although here the equi-
valent of regulatory energy is the total amount of expansive energy. A mammal
that gains much more energy than an earthworm isn't as fit, on any time scale,
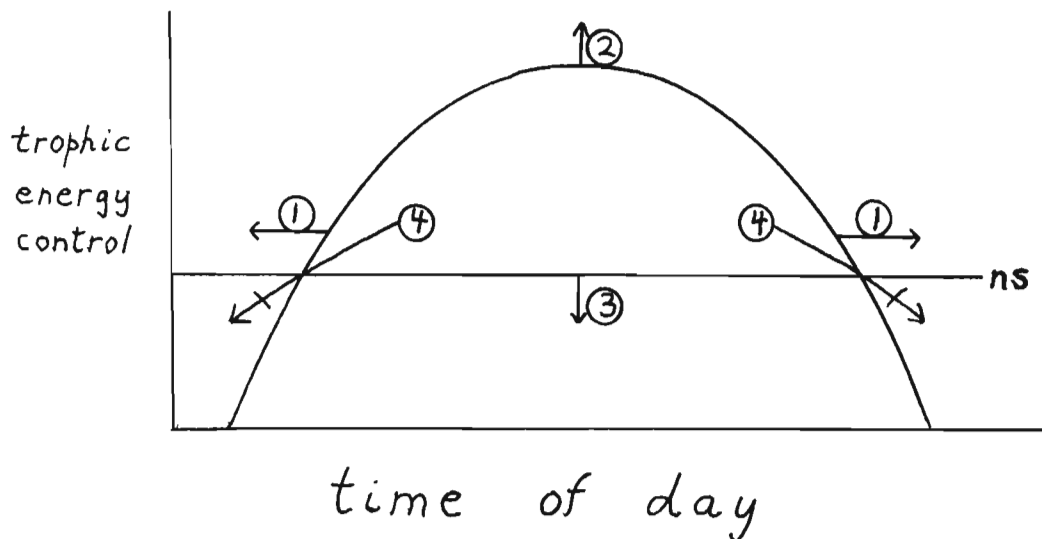
Fig. 7. The four ways in which a population can increase its regulatory
energy. 1: Extension of favorable region (limiting factors). 2: Increase
of total energy control (regulatory factors). 3: Lowering of line of expan-
sive sufficiency (direct factors). 4: Reduction in subsidy of unfavorable
regions.

    *   *   *

unless it gains enough for its own growth or reproduction. But still it is
useful to approximate the fitness of any unit by the total amount of trophic
energy it controls. This is, after all, the best measure of its direct effect
on the community. Moreover, how a species partitions its energy between main-
tenance and expansion is determined by natural selection at various time
scales. Individual selection that lowers the line of expansive sufficiency
of a population may also reduce its total energy control; it may even do this
for an individual. In Equation (4), $e(t)$ should be interpreted as regulatory
energy.

Therefore the third law of natural selection is best stated as follows:
Natural selection, at any level or time scale, maximizes the amount of regu-
latory trophic energy (88). But in the real world the earlier form of the law
is easier to deal with and the difference in application is probably negligible.
Natural selection acts so that as much as possible of the total energy con-
trolled is turned into regulatory energy. All else is mechanism to this goal.

A species that has little regulatory energy is near extinction, whatever
else it may possess. A quantitative statement would need to incorporate the
amount of expansive energy per individual and fluctuations. Species at dif-
ferent geological times can be compared in realized fitness by estimates of
their amounts of regulatory energy. But, as Darwin (1859) realized, an average
modern species can probably outcompete an average Paleozoic species because
of general adaptations. Therefore the expansive force at all relevant parts
of the adaptive space is also a major component of potential fitness.

A population can increase its regulatory energy in four ways (Fig. 7).
One is by enlarging its favorable region. (The favorable region of any group
can be taken as defining its adaptive zone.) This involves selection to over-
come 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. This is done by the selection on

(other) direct, and mostly on dominant, factors, and need not always be in the favorable region. Here it is necessary to note that the line of expansive sufficiency can be at different heights in different parts of the adaptive space, although I have drawn it horizontally for convenience. Because most individuals are clustered in the favorable region and natural selection favors the good of the most common (Van Valen and Mellin, 1967) (89), the line of expansive sufficiency for individuals should in the absence of other constraints be lowest near the center of the favorable region and rise, perhaps exponentially, in most directions away from this area. The last way for a population to increase its regulatory energy is by reducing its subsidy of unfavorable regions. Because this reduces the force of expansion and therefore effectiveness in competition, it is probably rare except in directions where there are no competitors, although I gave an example of it in a preceding section.

I have elsewhere (Van Valen, 1975b) compared the realized fitnesses of a palm, Euterpe globosa, and modern man, in terms of trophic energy control. They proved indistinguishable to an order of magnitude of kilocalories per year. If we assume, as a rough approximation, that all individuals of both these species occupy their respective favorable regions, it is then possible to compare their total amounts of regulatory energy. Regulatory energy then reduces to expansive energy.

For Euterpe, about 2.5 percent of the gross photosynthesis of a population is used for growth and reproduction (Van Valen, 1975b). This comes to 10^{13} or 10^{14} kcal./year for the entire species. For Homo sapiens, we can take the energetic cost of reproduction to be that of lactation and substitutes, because this is much greater than the cost of pregnancy. Moreover, the cost of later growth is negligible relative to that of maintenance. Therefore a rough estimate of the cost of reproduction is that of a lactation period of 2 years, for every surviving individual, including the effects of dead individuals in the computation as part of the cost of getting survivors. Lactation adds about a third to the caloric requirement. With a mean age of 30 years for living individuals, about 2 percent of human caloric intake is used for growth and reproduction. This also comes to 10^{13} or 10^{14} kcal./year for the entire species.

Therefore the comparison using regulatory energy comes to the same conclusion as that using total trophic energy: Homo sapiens has roughly the realized fitness of Euterpe globosa. I have elsewhere (Van Valen, 1975b) given minor qualifications to this conclusion.

By a minor extension of the Red Queen's Hypothesis, the average total amount of competition in a community is roughly constant (90). This is true for the average species if the number of species is also roughly constant (91). The amount of competition on a species is the biotic part of what I have called (Van Valen, 1973a) its environmental load and Maynard Smith (in press) has called its lag load. As both these papers show in different ways, biotic selective pressures on an average lineage through time will then vary about a single mean value. Abiotic selective pressures are much more intense at some times than others, whence (directly or indirectly) major and minor bursts of extinction sometimes occur. But the environmental load is sufficiently constant over long intervals of time that the mean rate of change of single proteins is rather constant, and a similar degree of constancy holds for the mean rate of change of single morphological characters (Van Valen, 1974b). Thus the ramifications of energy control pervade all of evolution.

Mystics and ecologists say that the world is one.

NOTES

     1. There are several points relevant to the constraint imposed by the
single oxidation of a given reduced carbon atom. Such an atom may leave the
community where it was originally reduced. The entire marine benthos, except
that close to shore, gets all its trophic energy in this manner. Such an
occurrence merely expands the domain of competition: members of two communi-
ties now compete for the same energy. Moreover, to the extent that no species
may be able to prevent the removal of energy from its own community, the amount
removed is irrelevant to competition within that community.

     Some carbon atoms are controlled sequentially by several organisms before
being oxidized. This fact does not affect the zero-sum conclusion because
the latter refers to control at any single time, or the integral of the
amounts controlled over some time interval.

     The actions of herbivores sometimes stimulate community photosynthesis
as well as sometimes reducing it (e.g. Flint and Goldman, 1976). Inter-
ference among plants can also reduce total photosynthesis (e.g. Lodhi, 1976),
and total photosynthesis can change as the species composition changes during
succession. This sort of phenomenon does affect the domain of the Red Queen,
although not strongly. A zero-sum constraint operates closely at any single
stage of succession, and also over the entire spatiotemporal mosaic that is
regionally stable but is at different stages of succession in different places.
There is no evidence, or even a suggestion, that interference among plants
has an appreciable affect on community photosynthesis. It nevertheless
possibly does so occasionally; the species involved would then have temporarily
escaped from the domain of the Red Queen.

     Herbivores would seem to have a more serious effect, but this also is
counteracted. If herbivores reduce total photosynthesis, they are acting as
a community-level regulating factor in the same way as, say, a shortage of
water. Both impose constraints on the community which exert selection pressure
(provide room for possible improvement) on all species equally, although some
species may respond better than others. Similarly, herbivory that increases
photosynthesis is also likely to be detrimental to the plants involved. The
increased photosynthesis is a response to bring them back to a level of fit-
ness near what they would have had without the herbivory. Again, there is no
evidence that herbivory ever increases a plant's fitness except in competition
with other plants that are more susceptible to being eaten.

     McNaughton (1976) has obliquely suggested such an increase in fitness, as
have others, but (as in McNaughton's case) the regrowth is normally to a lower
level than what would have been present otherwise, or there is a detrimental
effect on reproduction or growth. McNaughton also thought the regrowth after
feeding by wildebeest permitted gazelles to coexist with the wildebeest. But
the wildebeest could also have used the regrowth, as is potentially true in
general for the competitors of a herbivore that stimulates photosynthesis.
Moreover, there was still appreciably more green biomass in ungrazed patches
than in grazed patches. Therefore the amount of food under the observed con-
ditions was unlikely to regulate the density of either species, and it is thus
irrelevant to their coexistence.

     2. "Lose" is in the sense of failing to gain a possible benefit. Because
each species constantly uses energy, a failure to gain replacement energy,
and energy for reproduction, is equivalent to a loss.

3. Painter (1975) found it appropriate to devote an entire paper just to showing that group selection and individual selection give different optimal mutation rates, a point which had escaped Eshel (1973).

4. Any extinction of old groups and founding of new ones wouldn't affect Thompson's calculations. There is some selection at the individual level, on disease resistance and compatibility with other blood groups, and perhaps some prezygotic selection, but these are all weak relative to the overriding effect of group selection here.

5. It is evident that a greater control of realized trophic energy acts causally in evolution that proceeds by expansion of groups, in that such control permits a greater number of energy-converters to survive and reproduce. Such energy converters (individuals) might themselves expand, but this is ordinarily subsidiary. The case of Homo sapiens is unusual if not unique in that its total numbers aren't regulated now. For this species the energy argument is more obvious for the time before the industrial revolution but can be extended later by considering only energy intake, as other energy control is at this time not importantly related to population regulation.

6. A truism may sometimes have important consequences when it is not dismissed as trite.

7. A surrogate resource may be defined as a resource which is competed for in order to get more of another resource, this second resource being more valuable.

8. The commonly observed regulation of barnacle populations simply by space on which to settle, implies that all other resources (energy in particular) are in adequate supply relative to the barnacles' ability to get them.

9. Because Cactoblastis can eliminate any patch of Opuntia it finds, a less than perfect dispersal of Cactoblastis is critical to the survival of Opuntia. The greater the absolute distance between such patches, the longer the expected survival of a patch. That nutrients of any kind are no longer regulatory for Opuntia in Australia is shown by its dramatic decline in density when Cactoblastis was introduced. A thought-experiment shows the regulatory nature of absolute space here. Eliminate some of the space available to Opuntia, even if no individuals are now in the space removed, and close up the hole if the removal was from inside the range. The regional equilibrium number of individuals is then correspondingly decreased even if nothing else changes.

10. That factors other than trophic energy often regulate population density merely means that such populations have been unable to reduce the effect of these factors enough.

11. A barnacle would be selected to give up some of its settling space if part of the population is thereby enabled to become neotenously planktonic throughout its life and gain more energy for reproduction than it could while sessile. Some barnacles have in fact abandoned a sessile life for greener pastures elsewhere.

12. Plants in poor soil often have a low leaf area index, the ratio of leaf area to ground area (Tamm, 1975). They also maximize their control of sunlight by maximizing their control of surrogate resources.

13. Another useful partition is between trophic energy which is degraded to heat energy by the referent evolutionary unit, and trophic energy which it does not itself degrade but which it keeps others from degrading.

14. The defence of reserve energy may be imperfect, especially against very different kinds of species. A territorial bird may be quite ineffective in preventing insects or fungi from eating its food, even if the territory's main value is its food.

15. Waste energy includes part of assimilated energy. The adaptively-based partitioning I use cuts across the usual one, which is based on physiology. Losses due to phenomena such as attrition, physical accidents, parasitism, and death of component units are excluded from e_c because the latter is time-specific rather than cumulative. Parasitism is an aspect of competition for the same trophic energy.

16. The relevant expansion on the individual level is of the set of genes related by descent. Alternatively, it is of the phylad formed roughly by the individual and its descendants. Coefficients of kinship expand the phylad somewhat with partial inclusion of other individuals.

17. Energy is transformed, not used, but the latter expression is convenient when "energy" is itself measured by reduced carbon and the equivalent. The relevant energy is (Gibbs) free energy, the change in which is the energy output of an ordinary irreversible chemical reaction at constant pressure. The total potential chemical energy in an oxidizing environment is a little larger, but the difference is probably unimportant for ecology. Broda (1975) has a useful discussion. An additional minor qualification is that the potential energy of reduced carbon varies with the oxidation potential of the environment; even in reducing muds some animals migrate to the surface for oxygen.

18. The relationship of trophic energy to entropy is obscure. Schrödinger (1945) noted that organisms feed on organized energy. Equating entropy with disorganization, as Gatlin (1972) has done beautifully, Schrödinger then said that organisms feed on negative entropy, which Brillouin (1949) shortened to negentropy. But in thermodynamics entropy is rather independent of free energy, the difference between total energy and entropy (divided by temperature) being free energy. Moreover, organisms don't use all aspects of negentropy in their environment, such as earthquakes or the pattern of cracks in a drying playa, nor even in most cases pure carbon, and they do sometimes use heat in activities like sunbathing as a substitute for some trophic energy (Van Valen, 1973b). I suspect that some conceptual revision will be necessary before entropy can find a useful place in ecology. Wiegert (1968) in fact thought the use of entropy is superfluous in ecology, and Smith (1975) agreed with Wiegert from a somewhat different (if historically muddled) approach. However, because the irreversible degradation of energy to heat is the basic application of entropy, and this is another and possibly more fundamental way of looking at the use of energy by organisms, such a conceptual revision could prove important.

19. Reserve energy has no necessary dependence on time, but it is scaled to conform with the other quantities by determining how many units of time it could sustain the observed turnover. Thus if $e_d + e_w = x$ kcal/day and $e_r = tx$ kcal, $e_c - e_s = x + tx$ kcal for each day. The same sort of relation holds for structural energy. Because the unit is energy per unit time it should perhaps be called power rather than energy, but the latter term seems more appropriate for use when reserve energy and the like must be considered.

20. r_t, the trophic rate of increase (Van Valen, 1973c), is the rate of increase in numbers of a population at optimal density in a real environment, when the effects of competitors and predators are excluded.

21. Population size can also be expressed in energy units, in which case n should be replaced by b in Equation (3). This equation is subordinate to the verbal definition of expansive energy and has a narrower domain.

22. Endotherms use more free energy than do ectotherms, which is in itself a disadvantage (Van Valen, 1973b). They are selected to do so not because of the greater total energy control made possible but because endothermy provides more expansive energy under some circumstances.

23. With selection of gametes, chromosomes, mitochondria, or the like, one must merely realize with Samuel Butler (1877) and August Weismann (1883, 1889) that the hen is an egg's way of making another egg. Successful chromosomes reproduce and their offspring control the formation of bodies which control energy.

24. Apparently nonselective change in numbers is ordinarily selective in a broader domain.

25. Relative selection can still be used with energy, but a treatment in absolute terms seems more natural.

26. The necessity to consider expected values in fitness is periodically overlooked. A recent and deliberate example is a paper by Hirshfeld and Tinkle (1975). They equate actual survival with expected survival, and therefore conclude that the expectation of future death doesn't affect the reproductive value or strategies of individuals because it doesn't affect the reproduction of survivors. This strange conclusion seems to result from a rigidly frequentist interpretation of probability. Other interpretations of probability (e.g. propensity and subjective) permit probabilities of single events and therefore permit expected survival to have meaning for an individual. It obviously does so both in natural populations and for ourselves. We must not let theories tell us that obvious facts are wrong; in such a case, as here, the theories themselves are suspect.

27. The deductive derivation of the third law may seem to be circular. An assumption in the derivation is that a greater control of trophic energy results in greater expansive energy, yet this will be true only if natural selection maximizes expansive energy, which is the third law.

The apparent circularity does not, however, lie in the deduction. It comes from the causal process itself, which maps itself onto the deduction. Circular causal systems present no difficulty (Hutchinson, 1948). They are at the ontological level. The epistemological level is where the deduction occurs. How we know that a greater control of trophic energy gives more expansive energy, is (or can be) independent of the third law.

28. Frequency-dependent selection would also seem to provide a restriction on the domain, but this is probably only formal. There may well be no real cases that are not also covered by one of the other restrictions and that do not involve different use of resources or differential predation. The latter two classes of cases are part of the domain.

29. The phenotype of the tree has been shaped by natural selection at much longer time scales than an individual lifetime, so there is no reason to expect a strong relationship at the time scale of an individual. It is important to note that maximization of expansive energy is expected only at the time scale of the selection being considered.

30. Either the amount or the proportion of trophic energy control that natural selection changes can be either realized or potential, by another subdivision of natural selection.

31. The selection is among species rather than within species; terrestrial species are locally favored rather than "encouraged".

32. Thus the time interval considered also involves an ontological and necessary fuzziness, and here too it may eventually be possible to make precise the nature and conditions of the fuzziness (cf. Levins, 1964, 1968). An unrepeated environmental change is a selective force for directional adaptation, but a cyclic change of the right amplitude and periodicity selects for phenotypic tolerance. And either response may affect the probability of extinction. Moreover, one can't specify the time of evaluation to be immediately after the selection, because selection may be on something like fecundity which doesn't immediately manifest itself in energy control.

33. Within a group of individuals having the same generation length, absolute time can of course be ignored and the more convenient unit of one generation can be used. That this is usually done, and even incorporated into some concepts of the nature of natural selection itself, must not blind us to its lack of generality. Various workers (e.g. Charlesworth and Giesel, 1972) have treated within-population selection where generation lengths differ among individuals. Differences in generation length are even more important in selection among populations and taxa.

34. The conflict is commonly stated as being between levels. Nonregulating phenotypes ordinarily increase in a population at the expense of phenotypes which limit their own offspring in response to density. Yet a self-regulating population would be less liable to fluctuate in density and therefore usually less liable to extinction. From the viewpoint of time scales, however, we can note that the probability of extinction increases with time. Therefore the advantage of self-regulation also increases with time, because its advantage is resistance to extinction. That no self-regulators may have escaped the short-term selection is irrelevant to the long-term advantage for any which could. Williams (1975) has treated self-regulation from the viewpoint of time scale. Selection at different time scales can produce equilibria in exactly the same way as selection at different levels (Van Valen, 1975a). Greater body size usually is an advantage to mammals and foraminiferans on geologically short time scales but a disadvantage on longer time scales, where entire groups with larger body size are more prone to extinction without issue. I treated this as an opposition of group and individual selection, which it is, but it can also be viewed as a situation where individual fitness is in different directions at longer and shorter time scales. The same analysis holds in each case, as it must because the only difference is in how we look at the processes.

35. Because the weighting function is arbitrary, the value of fitness is also in part arbitrary. This is where the quantification of the necessary imprecision of adaptedness and adaptability comes in. However, the expected or realized fitness ($e(t)$) after a given period of time is required in determining the action of selection at that interval.

36. Templeton and Rothman (1974) showed that Lewontin's distinction between maximin and maximean evolutionary strategies does lead to different consequences in the two cases, although they failed to cite Lewontin's paper. But they then tried to find a single optimal strategy on all time scales and claimed that this will usually be a mixture of the two extremes. However, simultaneously maximizing any two or more different parameters when there is more than one way of weighting them, is well known to be impossible. A given strategy, often intermediate, does result in each case from the past operation of selection at different time scales. But to say that such a strategy is optimal is to say that a single weighting function is appropriate. For the present adaptations of a species, at one point in time, one would want to do this, but comparisons either over geologically long time intervals, or among different lineages, among which selection also occurs, show that a generally applicable function is unavailable.

37. By "adversely affected" I mean having a lower fitness (expansive energy) than would be the case without the competitor.

38. The first proof does not, of course, apply to specific sets of organisms such as clams, but rather to the entire local community in which they are embedded.

39. Peter Yodzis has kindly pointed out that I was mistaken when I said (1974a) that the equilibrium between individual-level competition and predation should be excluded from my treatment of equivalent predation. At moderate

levels of predation this mechanism, which is equivalent to the stability-
time or fugitive-species mechanisms, permits coexistence of a few species
under equivalent predation. By definition it involves competition in a major
way.

40.   The stress-competition equilibrium includes as named special cases
the stability-time hypothesis (Sanders, 1968, 1969; Slobodkin and Sanders,
1969; Grassle and Sanders, 1973; Margalef, 1968; Johnson, 1970, 1972),
fugitive species (cf. Dayton, 1971), colonizing species (Levin and Paine,
1974, have a recent treatment), and probably most or even all real examples
of the immigration-extinction equilibrium. Most of these references give
evidence on applicability to clams as well as giving theory.

41.   Energy flow can be high with a low standing crop, however, as with
the plankton and other communities that have a rapid turnover because of
predation, and Jackson gives no evidence on this point.

42.   From the Red Queen's viewpoint, Ghiselin (1974) has noted that
"predator and prey compete for nutrients and energy".

43.   An analogous treatment is possible for other kinds of competition
than for one resource. By a resource I mean anything which is needed by a
population or individual, or at least which enhances its fitness.

44.   T of course uses different individual holes or molecules or food
individuals than S does; the overlap is in their similarity to those of S.

45.   I discuss evolutionary response to competition in a later section.
The amount of competition may be either realized amount (the immediate gain
if the competitor were removed) or potential amount (the gain at evolutionary
equilibrium after removal of the competitor), or it may have some intermediate
value.

46.   No conclusions in this paper are changed if e_a is substituted for e_p
in the denominator of Equation (5). This is a little cleaner algebraically
(e.g., then $P = A/R$) but seems less useful biologically.

47.   In deriving Equation (6), one must realize that A and R are both
ratios, not amounts of the resource, and that their denominators differ. The
basic definition of P is the ratio of the dotted area in Fig. 1 to the ruled
area.

48.   The total expansive force of a population is the rate of flow of
energy out of its realized favorable region in the adaptive space. When
there is much overlap between adjacent species for a resource in at least
relative short supply, the energy remains in the unfavorable region (e.g.,
individuals survive there) longer than it does when there is little overlap,
when the competitive pressure is higher. In the latter case the competition
functions (defined in a later section) of the two species are more different.
The expansive force of a species exists so that the species can take over
energy not used by a competitor as well as to minimize encroachment by the
competitor. Thus the more energy a species loses to a competitor, the greater
the resistance of the referent species to further encroachment as long as the
encroachment isn't overwhelming. And this is true whatever the pressure of
competition. But the encroachment measures the realized amount of competition.
Therefore the realized amount of competition probably varies less than the
pressure or overlap.

49.   The effects of fluctuating environments are beyond the scope of this
paper. Preliminary work suggests that they extend the conclusions of this
paper rather than modifying them importantly.

50.   Timin and Collier (1971) reinterpreted the classical equations of
population growth in terms of energy units, and Roughgarden (1971) translated
part of the standard theory of natural selection into these terms.

51. The common use of "limiting factors" to include regulating factors glosses over a fundamental distinction (cf. Haldane, 1953). Temperature, for instance, can limit a species' range, but in itself can do nothing to regulate the species' density within that range, i.e. to determine how many individuals (or the equivalent in energy control) can occur in any place where they can occur. Refuges from temperature extremes can, however, be regulatory, and very short-lived populations would be an exception on the population level but not the regional level.

52. The precise condition is an increase in the average intensity of the factor per individual.

53. This way of looking at competitive exclusion is vaguely similar to that of Smith, Shugart, O'Neill, Booth, and McNaught (1975). They conclude, however, that in an equilibrium community all competitors are about equal because they all persist. This conclusion holds only at the critical points.

54. On the difficulty of determining the necessary conditions for such a proposition, and therefore bounding its domain, see the beautiful treatment by Lakatos (1963-1964). The domain nevertheless seems to be large and to embrace a very large majority of cases of coexistence or its lacks. Some authors believe that showing any case of failure of the principle of competitive exclusion invalidates it or makes it unimportant. However, this is merely a defect in their logic. Most true propositions have less than universal domains.

55. The curious lack of recognition of the basic relationship between density regulation and competitive exclusion is exemplified by a review of niche theory and coexistence by Vandermeer (1972), who didn't even mention regulation.

56. Convergence, like other evolution, must of course be permissible developmentally and have a net overall advantage.

57. Convergence of sympatric species, such as the presumptive cases of Rosenzweig (1968) and Berry (1975), are necessarily for adaptations which don't affect coexistence and competition. The evolution of such characters is much slower than competitive exclusion.

58. I discuss in a later section boundaries of realized adaptive zones which aren't caused by competitors, but such boundaries have no compressive force because they coincide with the corresponding edge of the potential adaptive zone, except for possible response to changes elsewhere.

59. The difference in height of lines of expansive sufficiency determines the outcome of exploitative competition between phenotypes in the same adaptive zone. Social effects can modify the height of the line, which therefore will sometimes depend on density.

Vance (1972) showed that the availability of empty shells regulates the density of three species of hermit crabs. Their coexistence is facilitated by their having somewhat different habitats, and Vance thought that this makes an analysis in terms of the regulatory resource inapplicable. I hope the present discussion shows why the regulatory resource is still basic in their competitive coexistence.

60. The term from physics shouldn't be taken literally, as I use it to minimize the coining of new terms. In physics, force of course isn't measured by energy.

61. Dispersal (or, equivalently, fluctuating environmental patchiness) is also relevant to the force of expansion, in that a phenotype must be at the physical location of its potential competitor in order to compete. Regionally, however, this effect can be subsumed in the competition coefficient by defining "together" to mean "regionally together". The effect is well enough analyzed in existing theory that I will not pursue it. However, it is useful to realize that dispersal can be an aspect of competition when viewed more than locally.

62.   If a phenotype is ultimately regulated at one stage of its life cycle, its expansive force is determined by that regulation. If young and adults eat different foods, say, and regulation is by food for the young, then only the young are relevant in competitive exclusion and adults may have a surplus of food and other resources. Neill (1975) has a nice example of this for crustaceans.

63.   Interference can occur irrespective of proximity in the adaptive space. However, interference isn't always competition. In some cases neither species gains anything. This is the expected result for many cases of susceptibility of species of the soil microflora to antibiotics: surely most such species aren't competitors of the producer of the antibiotic. The interference is then adaptively accidental, and there is a net loss of fitness to both species on the basis of this interaction alone. It is therefore an example of the rare class of interactions sometimes called spiteful and whose existence is sometimes questioned.

64.   Variation in realized fitness is greater in unfavorable regions partly because the effect of predation may be greater, but partly because buffering against environmental stresses evolves mostly for those stresses that affect the most parents. Such stresses are those of the favorable region. Random effects (i.e. those for which adaptations haven't evolved: probability and randomness are always relative to available information) should therefore be greater in unfavorable regions.

65.   Because of the greater density of individuals in the favorable region, the mean fitness of individuals there may be below the line of expansive sufficiency. Some individuals in both regions will usually have expansive energy. However, if some individuals move to an unfavorable region, the remainder may benefit more than the dispersers. Such movement happens even in nonterritorial species (Dethier and Mac Arthur, 1964); perhaps the threshold density for dispersal or other movement in adaptive space is greater than the density of equal expected fitness.

66.   Haldane (1953, 1956) discussed differences in selection pressures acting on central and marginal populations, and Carson and Mayr have been his most prolific followers on this point. Haldane's distinction is included in mine at the species level, but I include also other shifts in adaptive space than those due to physical location, and I extend the concept to local populations.

67.   A diversion of expansive energy into a less unfavorable region might happen immediately for a behaviorally flexible species. If food A is scarce because of the new competitor, or the new competitor interferes with the referent species, such flexibility might result in a shift to food B or out of physical range of interference at the individual level. Communication would help the efficiency of such a shift.

68.   Character displacement (the response to selection for reduction of overlap) isn't restricted to regulatory factors. Color patterns can diverge to produce different search images for visual predators, eating habits can diverge if food is sometimes relatively scarce even though nesting sites are regulatory, and so on.

69.   Because any stress (factor reducing fitness) produces a selective vector that will be responded to if the species is capable developmentally (and in variation, usually a negligible condition), there is no problem in principle for the species to increase its competitive ability.

70.   Individually plastic behavior permits such a response in some organisms: this is one way to look at the establishment of territories in suboptimal areas with little change in the rest of the adaptive space occupied. Without plastic behavior, diversion can happen only on the time scale of selection.

Movement of energy into the region of overlap is selected against because of the reduction in fitness there due to the competitor. The energy then can accumulate in the favorable region and be part of density-dependent regulation. However, this greater density in the favorable region itself selects for subsidy of unfavorable regions, as it always does. Therefore part or all of the reduction in subsidy of the region of overlap may be diverted to a less unfavorable region. The selective relationship is the same as that for flexible behavior, but the different mechanism for its realization takes more time.

71. Note that selection is potentially most important with respect to whatever influences cause the greatest reduction in potential fitness (Van Valen, 1973c).

72. Width of adaptive zone affects population fitness directly, as it is an important determiner of control of trophic energy. But since trophic energy isn't uniformly distributed in adaptive space, some species with broad adaptive zones (not synonymous with euryphagy or eurytopy: the axis is of ultimate population regulation) may be less fit than some species with narrow zones. Such modality of the adaptive space is presumably the main reason why the boundaries of adaptive zones are often, but not always, clustered (cf. Van Valen, 1973d; in press).

Species packing, like much else, is beyond the scope of this paper.

73. The rate of response to the disappearance of a competitor of course depends on the adaptations involved.

74. Many species coexist in biotically accommodated habitats by assumption. Because of the assumption of relative stability of the habitat, these species are able to adapt well to relatively small parts of the adaptive space at the expense of broader adaptations. Thus low overlap is expected but not a low amount of competition. Therefore competitive pressure is high.

75. In physically controlled habitats the variability of the environment prevents precise adaptations, both directly and by effects on species interacting with the referent species. The breadth of adaptations required means that overlap ordinarily should be large, and there is no reason for the amount of competition to be unusually large. Therefore competitive pressure is low.

76. Pianka (1971) noted that r-selection is associated with "variable, often lax" intensities of competition. Possibly he was thinking of the same sorts of cases I mention, although he didn't justify his statement or even specify what he meant by lax competition.

77. An early successional species has large overlap with its successors in some ways but not in a resource critical to its regional survival, namely newly open patches of habitat. And more importantly, the species has no chance to overlap its successors in places they already occupy. But this physical space (with associated energy) excluded from the region of overlap is mostly or entirely available to the colonizer if the successors were absent. The amount of competition is thus extraordinarily great while the overlap is only moderately large. Therefore competitive pressure is high.

Pressure isn't symmetrical among species because the amount of potentially available trophic energy actually controlled by a competitor may be very different, as in this case.

78. Gilroy (1975) showed for Simberloff and Wilson's (1969) data on recolonization rates of minute islets that the extinction rates fit the expectations of noninteractive equilibria. However, Heatwole and Levins (1972), whom Gilroy didn't cite, had showed that the recolonization was trophically balanced. Therefore the equilibria even in this extreme situation were importantly interactive.

79. It is usually more difficult for a species to defend a large favorable region than a small one because of developmentally and functionally conflicting

adaptations. This is why fitness functions (Fig. 2) have whatever shapes
they do have rather than being broader. The number of species that can coexist
depends on the positions of their critical points. These positions are deter-
mined by the competition functions of each species relative to its neighbors
in adaptive space. And the competition functions depend on the ability to
mobilize expansive energy at various points in adaptive space. Therefore the
competitive ability of a species is well approximated by the shape and abso-
lute height of its fitness function. If the energy throughout the adaptive
space is reduced proportionally, the heights of all the fitness functions
decrease. The species are then more extended ecologically than they were
initially, relative to the energy they control. Just as is the case with more
energy, a broad fitness function is hard to maintain and is vulnerable to
narrowing or even elimination. Therefore there is room at equilibrium for
more species with competition functions similar to those already present. The
geometry of competition rather than the absolute amount of energy controlled
is crucial. With an invariant geometry, more species can coexist when there
is less energy.

    This argument assumes that interference is no more common in the deep sea
than in shallow water. Because the energy requirements for different kinds of
interference often decrease less than the energy available, I suspect that
average interference declines with depth. Predator defense may, however,
increase with depth, as Janzen (1974) argued for the partly analogous situa-
tion of tropical forests that grow on white sand.

    80. The density of at least metazoans on the floor of the deep sea is
lower than that in shallow water. This suggests that the average lowering of
the lines of expansive sufficiency is proportionally less than the reduction
in the availability of trophic energy.

    81. If the lines of adaptive sufficiency weren't lower in the deep sea,
probably few or no metazoans could occur there. But this contingency doesn't
affect the argument about diversity when the lines are lower.

    82. Whether a region of constantly high productivity would eventually
have unusually many species is unclear. The usual argument is that narrower
adaptive zones are then permitted because species need only be narrowly
adapted to get enough energy. But if the extra energy is concentrated in
only a small part of the adaptive space, one or a few species could thrive
on it indefinitely and exclude others.

    83. General adaptations are adaptations useful in a wide variety of
adaptive zones. Thus they are useful for many groups. The concept has nothing
to do with ecological generalists, phenotypes that themselves have broad adap-
tive zones. Clams have had some rather general adaptations, but the revers-
ibility of most implies that these adaptations are less general than, say,
increase of brain size in mammals.

    84. Rudists usually made their own reefs. Stony corals fail to show a
higher rate of extinction than other sessile groups of marine benthos (Van
Valen, 1973a). Other groups of clams (Levinton, 1973) as well as of mammals
(Van Valen, 1973a) show differences in extinction rate; the reasons for these
heterogeneities are not well understood.

    85. The transfer of expansive energy from one side of the favorable
region to another can perhaps be transitive, continuing through more than one
ecologically adjacent species as each responds to changes in its own competitors.

    86. Dayton (1973) and Van Valen (1975c) have discussed in an ecological
context the generation of true predictions by false hypotheses.

    87. Much of evolutionary biology has a deductive structure. Biologists
have been brainwashed by philosophers of science, who model their philosophy

on physics, into thinking that deduction is useful only to generate predictions. This is nonsense and has probably prevented much progress.

88. Density-independent effects can reduce the amount of regulatory energy and so are selected against.

89. When adaptations conflict with each other and each is of the same advantage to an individual, the adaptation that affects more individuals will be favored. The same argument applies to conflicting adaptations that are useful for different periods of time but are equally useful per unit time when they are effective.

90. The hypothesis of average constancy of total amount of competition says nothing about overlap. If each unit of trophic energy can be used by more than one species, and if effectively all such energy is used, then all energy in the community is competed for. Therefore it is all included in the amount of trophic energy that could be used by some members of the community if other species were absent. The denominator of the fraction representing the amount of competition in the community could then be designated as either the same amount of energy or twice this amount. The total amount of competition so defined differs from the sum of the amounts on each species because more than two species may be able to use the same energy. I assume that such additional potential use (by a third species or beyond) is either relatively constant or is a small part of the total trophic energy.

91. A direct argument for approximate constancy of the amount of competition on an average species can be made in a way like that of note 48.

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