

Levels of selection in the early Cenozoic radiation of mammals<sup>1,2</sup>

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**ABSTRACT:** I present a different way of looking at evolution and exemplify it with the Paleocene radiation of placental mammals in North America.

The biotic world is, among other things (but basically), a system of energy flow. For any community or larger biota we can consider this flow itself and ask such questions as how it is partitioned, what causes and regulates the flow and its partitions, how these change over time at various scales, and what processes cause these changes. A partly new approach to levels of selection, involving taxon selection, lets this paradigm be applied to the mammals.

Several levels of selection can be distinguished in the mammalian radiation. I quantify this for taxonomic composition and trophic groups; other partitions are also useful. Large differences exist for some comparisons of the amount of selection (a new measure), but in other cases none are detectable. The processes causing the selection also vary appreciably. The uniquely low amount of predation in the early part of the Paleocene implicates competition as the initial organizing force of mammalian communities.

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I want to present a different way of looking at evolution -- actually several different ways, but they are related, even though this may not be initially obvious. I will then, eventually, indicate how the Paleocene radiation of mammals empirically fits into this general approach. Innovations occur in communities and large-scale biotas as well as in lineages, and my focus will be on these innovations.

Most of us, I trust, no longer think of evolution as sufficiently described or caused, in a fundamental way, by changes in allele frequencies. But we can go further. I want us to ignore species, ignore individuals, ignore genes, ignore phenotypes: we may get back to them, but if so it will be secondarily. Back to basics, as the saying goes.

Our first concern is with life itself, with the flow of free energy which powers it. This can be in a local community, or worldwide, or at some intermediate breadth. We view the biotic world as a system of energy flow. We ask in what ways this flow is partitioned, what causes the flow and its partitions and regulates the

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<sup>2</sup>This paper was accepted in 1988, after review, for publication in the book *Evolutionary Innovations*, edited by M.H. Nitecki and published by the University of Chicago Press. The Press waited to send contracts to contributors until it was ready to start printing. The Press insisted on keeping in the contract a provision which insisted that I promise to reimburse them for the full cost of any (even frivolous) lawsuits, while they retained all authority as to proceeding with or settling them. If such a lawsuit has a negligible probability it should be no hardship on the Press to modify it; if the probability is not negligible then the inequity becomes meaningful. The policy, also adhered to by some other publishers, is widely regarded as grossly unfair, and it is only by authors objecting to it that it can have a chance of being modified.

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various rates of flow. This sounds suspiciously like systems ecology, and the resemblance is real although the categories and methods of systems ecology may often be inappropriate. The study of food webs and other topics are also relevant. We then ask how the partitions and flows change over time, at both ecological and evolutionary time scales, and what processes cause these changes.

To the extent that this suggestion has merit, it replaces genetics by ecology as the central causal subject of the evolutionary half of biology. Furthermore, it is probably appropriate to think of supramolecular evolution as being directed mostly by movement of the phenotype x environment adaptive landscape (on which see Dodson, 1975). The evidence from the bloom phase of adaptive radiation (Van Valen, 1985b), as well as other considerations, suggests that genetic (as distinct from developmental) constraints are rarely important in real evolution. From this perspective, too, ecology replaces genetics as the central causal subject.

The above program is possibly a bit too ambitious for one paper. My main purpose is to indicate that it is both meaningful and workable. In order to do so we need to look differently at levels of selection.

### Levels and Time Scales

There have been several kinds of criteria proposed to distinguish levels of selection. These criteria have been meant as mutually exclusive, so what is, say, group selection by one criterion is regarded as ordinary individual selection by another. But we don't need to do this: the distinctions are usually real ones and indicate a lack of sharp boundaries between levels.

An analogy with population ecology may help. Population regulation is the central process of the phenomena of population ecology; if anything is population ecology the study of regulation is. However, looked at in another way it is completely accounted for by things that happen at the individual level: individuals die, reproduce more rapidly, or whatever, as a result of things that affect them individually. However again, an individual has a greater probability of dying per unit time in a higher population density: the density is a cause of its death. (See Hardin, 1971, for an example interpreted this way.)

Similarly with extinction. A genus goes extinct when all its species go extinct; a species goes extinct when all its populations go extinct; a population goes extinct when all its individuals die. So it looks as though selective extinction is a kind of individual selection, and indeed it has been interpreted as such. But it is more than this. The probability of extinction depends partly on the number of individuals in the population, a population-level trait. More importantly, the individuals or species aren't random in a larger context; because they belong to a natural group they tend to share the attributes which make the group natural. A genus, for instance, has characters which (in taxa where the study of functional anatomy is more than rudimentary) can commonly be related to particular adaptations. Its species don't go extinct independently. Some may eliminate others, but more importantly they will all tend to be susceptible to the same sorts of stresses of the physical and biotic environment.

All levels exhibit this. A group is natural because of kinship and adaptation. The relative importance of these two aspects differs depending on what processes or phenomena one is considering, so synthetic classifications incorporate both aspects. Selective extinction can indeed be reduced to individual selection, but what we lose in doing so is important in the groups' interactions. We can reduce individual selection to genic selection, but again we have lost any more than a formal appreciation of interactions. There is no single basic level of selection, and indeed the levels themselves partly intergrade with each other.

The same is true for different time scales. As has long been realized, mass extinctions and normal extinctions select for partly different sets of properties. Even within a period of normal extinction a character advantageous in short

intervals may be disadvantageous over longer ones. (The reverse situation, with a character advantageous over long intervals and disadvantageous over short ones, is a temporal analog of altruism and has similar problems in establishment. I don't think it has ever been studied theoretically, and the conditions for establishment or equilibrium would be nice to know under diverse circumstances. Obviously direct and indirect selection and drift are involved as well as the analog of mutation.)

By long-term selection I don't mean merely that from rare events, even noncatastrophic ones. Short-term adaptation can reduce the possibilities for future responses. This is too well known to belabor; it used to be called change in adaptability before the terminology of constraints came upon us. We should note, though, that individual selection tends to merge into group selection as we go to longer time scales. For instance, large mammals occasionally evolve from small ones but rarely (except on islands) reverse this trend. The same is true for foraminiferans. Is this individual or group selection? Does it matter, i.e. is there a real distinction to deal with here? Genera of large foraminiferans become extinct more rapidly than those of small body size, while large body size in mammals inhibits generic branching (Van Valen, 1975). In each case large size gives a net long-term disadvantage at the group level. Although body size is not what one would call an emergent group property, it causes group selection.

Some individual selection is better for a group than is other individual selection. This provides a basis for selection of the groups species or lineages or clades or families.

There is in the received viewpoint of evolutionary theory an implicit assumption that one individual is equivalent to another as a unit (not necessarily equivalent in fitness, of course) and that there are natural units identifiable as individuals in the first place.

For individual selection in *Drosophila* or mammals, it is a reasonable approximation. It is not reasonable for group selection at any level, unless things average out appropriately, as we will see that they sometimes do. It is not reasonable, again, for reef corals or for trees or for many other organisms. These are all what I have called somatogens (Van Valen, 1987), organisms which do not have a single germ line from which all reproduction occurs sexually. There are two kinds of somatogens, clonates (which form clones) and polygenerates (which have more than one germ line).

### Expansion

An important means of competition for many somatogens is individual expansion. (Contraction is negative expansion.) Size is important in natural selection, and not just for its consequences of greater reproduction and such. The expansion of a sponge at the expense of an adjacent bryozoan is natural selection, but it occurs with no death and no reproduction. If a branch with completely green leaves grows more than one with variegated leaves, that too is natural selection. A plant or a graptolite may grow out, or it may put the same energy into sending forth a new ramet or into sexual reproduction. In each case its goal, and it is a nonconscious goal (Van Valen, 1984), is to acquire more useful energy. Yes, Bertrand Russell (1927, p. 27) said it too: "Every living thing is a sort of imperialist, seeking to transform as much as possible of its environment into itself and its seed." Our theories can make us forget the obvious.

Such non-Weismannian evolution applies to groups too. Somatogens seem to resemble groups in the relative importance of their fitness components. A major mechanism of group selection is differential expansion. That is, e.g., why blood group A is decreasing in our own species at the astonishing rate of about 1 percent (5 percent of its actual frequency) in 35 years (Van Valen, 1976): this is a correlated effect of selection on cultural characters of groups. Similarly, Wright's intergroup selection (1932) operates primarily by differential expansion.

A population can, at least in principle, produce more populations just by subdividing itself. There are then more populations but even jointly they probably play a smaller role in the community. Our theories would nevertheless say that the lineage now has greater fitness. Vrba (1981), in fact, made about this interpretation for two clades of antelopes, one of which has many species branches and the other only one. Yet today the latter clade, the impala, apparently has about as many individuals as the former; as Vrba herself (1983, 1984) later noted, it doesn't seem less fit. Yet again, an individual impala is less than half the size of an average member of the other clade; the same number of individuals would use rather less energy. Treasure your exceptions: like an old tree, deeper penetration may reveal less substance.

Another example: A group A can gradually overwhelm group B by an increase in the size of its component parts, while group B increases in numbers of parts until near the end. This is partly what happened in the 30-million-year extinction of the multituberculates, an ancient order, by their placental competitors: the maximum diversity of multituberculates occurred several million years after the effective beginning of the competition (Van Valen and Sloan, 1966; Krause, 1986). The use of numbers of species gives a non-monotone curve for what is really a steady process.

Is a grass that is colonizing a new field by ramets automatically much less fit than one that is colonizing a field by seeds? In the first case one individual, in the sense of a genet (Harper, 1977), is expanding, even though it may eventually lose connections between clumps, while in the second there is lots of reproduction and new individual genets. Or compare the fitness of the parents of a tree and of  $10^2$  or  $10^3$  herbs covering the same area: are the parental trees  $10^{-2}$  or  $10^{-3}$  times as fit?

It is also now realized that for many plants, corals, and other somatogens, body size is more important than age. And further, in population regulation the standard theory counts individuals. But it can hardly be the case that natural processes depend on how we define terms, and a large individual is not equivalent to a small one, nor an active one to one in dormancy. In this theory also, it is essential to eliminate counts of individuals from its basic formulation; energy flow provides the only universal and natural replacement.

Somatogens themselves bridge levels of selection, because the boundary between an individual and a group becomes fuzzy as our several criteria no longer coincide with each other. For some somatogens, notably obligate clonates and obligate mutualists, the boundary between a deme and a species becomes fuzzy. How, exactly, does individual selection differ from group selection for a clonate? Or from within-individual selection? Or deme selection from species selection? Clonates interact with nonclonates too; these questions are primarily of processes rather than of terminology. We must therefore recognize that levels of selection intergrade with each other at short time scales as well as at long ones. Even if there were no other reason to do so (and there are, both up and down), this conclusion forces us to look skeptically at the usual view of individual selection as the overwhelming most powerful level.

As Westoby (1983) put it, "The first imperative of success for a piece of genetic information is that tissue containing copies of it be made at least as fast as tissue containing it is lost. Whether a net profit of growth is accumulated within the individuals or as multiplication of individuals all the same size is a second-order question."

Expansion is an important component of fitness in the real world, and we ignore it at our peril (or at our theories' peril). In fact the other components of fitness can easily be subsumed under it, as the rest often are under reproduction. Rather than saying that natural selection is expected differential reproduction, we should say that it is expected differential expansion.

## Energy

How then can we resolve all this? After all, we can see what the course of events will be in each case, and there is always a single outcome in real natural selection (barring stochasticity and chaos). What is the universal currency that is used? What is maximized? Consider the expansion component of natural selection by itself. Expansion of what, exactly? What is causally involved?

Biomass has been suggested, and it is, more or less, what is relevant for the next trophic level up, to feed on. But mass is not for the most part causal within a population, or in competition. More mass *per se* is not important except maybe for butting sheep and such.

We know that energy drives the physiological dynamics of life just as it drives inorganic processes. (Technically, both enthalpy and entropy are involved.) I conclude that free energy (normally in the form of reduced carbon or its redox derivatives) is, in some way, the universal currency. It provides a uniformly available measure which, moreover, acts causally in the relevant biological interactions. I have discussed this general matter at greater length elsewhere (Van Valen, 1976); the present section partly summarizes aspects of that paper.

But there are various objections which need consideration. I do mean that the availability of free energy regulates populations. Sometimes it does, and probably it usually does for the soil biota, but under other constraints that organisms can't overcome in the available time (say too little phosphorus, or water, or a high predation risk) organisms do seem to maximize their energy control. This is not, e.g., the contrast of energy maximization with time minimization; both are involved in a more basic maximization. We can specify the aspect of the environment which each organism tries to incorporate into itself and its seed. Lotka (1922) had close to the same idea, about the time of the quotation from Russell. Surrogate resources are resources whose acquisition is selected for as a way of getting more energy.

As Egbert Leigh has commented to me, if life evolved elsewhere it would not necessarily need any of the specific chemical materials our life does, but it would need free energy.

Maintenance energy, including reproductive energy not put into offspring, is not maximized; in fact it is apparently minimized under the constraints applicable in any particular case. Nevertheless, this sometimes results in apparently wasteful maintenance, as with endotherms. But if they get more expansive energy by wasting more, that is what is selected for. Efficiency *per se* is not maximized.

What does seem to be maximized is the rate of acquisition of expansive energy, the energy used for growth and successful reproduction. This is the surplus energy above maintenance. (My 1976 discussion of "regulatory energy" was based on a misunderstanding of what the maintenance energy of a group is.) Several years ago there was a graffito in the men's room in the Zoology Building at Chicago: "Fatness is fitness -- Van Valen." This is actually an interesting caricature. Over a very short interval fatness is indeed fitness, but we are usually interested in intervals longer than that, where excess fat or other stored energy may sometimes interfere with survival or reproduction or even with further expansion. It is quite essential for us to consider the time scales of selection carefully and explicitly. Similarly, a cancer is selected within the individual on a short time scale, with different cell lineages being selected successively on the basis of different properties as the cancer progresses. Or a grass that grows more and then is cropped down to the same level as others is no better off on the usual time scale. The time scale and level of selection which we are considering determine whether growth or reproduction is more important. In many somatogens there is no sharp distinction between growth and reproduction; it is therefore dangerous to use a basic theoretical framework which depends on such a sharp distinction and which must create one arbitrarily even when it doesn't exist.

Table 1. Amounts of selection in the basal Paleocene, through 0.5 Ma.

Unweighted	Species	Genera	Families	Orders
Placentalia	28.5	40.7	20.5	39.4
Marsupialia	0.57	0.33	--	--
Multituberculata	1.33	1.06	0.71	--
combined	9.82	13.2	6.5	20.6
insectivores	2.93	0.53	0.18	0.35
herbivores	16.3	19.3	7.3	36.1
between trophic groups	1.46	1.48	1.34	12.7
Weighted				
Placentalia	58.4	76.3	21.9	13.1
combined	13.7	17.5	7.57	19.4
between trophic groups	1.33	0.74	0.67	6.35

In the values weighted by energy flow, a taxon of putative herbivores had a weight of 15, one of insectivores a weight of 3, and one of carnivores (later Paleocene only) a weight of 1 (see graphs of Damuth, 1987). The Marsupialia are all putative insectivores at this time and the Multituberculata all putative herbivores. Nevertheless, assignment to trophic class was done for each species individually. Amount of selection is the variance of the ratio of the number of descendant species (if any) to the number of their ancestors, at any particular taxonomic category. Amount is not a rate, so there is no adjustment for time.

As an example, there are 7 species lineages of marsupials known at the time of Bug Creek Anthills, the earliest zone: *Pedimys cooki*, *P. elegans*, *P. florencae*, *P. hatcheri*, *Glasbius twitchelli*, *Alphadon marshi*, and *A. n. sp.* Only *A. marshi* has descendants at the time of the unpublished Alexander locality (Middleton, 1983), the latest zone, namely *Peradectes pusillus* and *P. n. sp.* The ratios of the numbers of descendant species over this interval to their ancestors are then 0, 0, 0, 0, 0, 0, 2 when grouped by species and 0, 0, 1 (= 2/2) when grouped by initial genera. The variances of these sequences are 0.57 and 0.33 respectively. As I put all 7 initial species into the same family, there is no selection possible at suprageneric categories. Ma is million years.

Taxa whose later status is unknown were excluded. There are 26 initial species used for the early interval and 87 for the later one. Multiple transitions from one initial taxon were counted separately. Eleven unknown species were interpolated in early lineages to fill large morphological gaps; they are included in the 40 phyletic transitions. In a branching, one branch was counted as an instance of phyletic evolution if both branches resulted in new species. Persistence means persistence through the whole interval.

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Likewise, populations are often at densities above that which maximizes their expansive energy, but this is again a conflict between group fitness and individual fitness. Each individual maximizes its own, and we have thereby a minor "tragedy of the commons."

Various people (e.g., Williams, 1966, 1986; Nunney, 1985) have regarded selection, particularly group selection, as a way to explain biological adaptations rather than as a process to follow wherever it may lead. So if process A can explain the adaptation, we don't need to consider process B. This is a particular case of the fallacy of null hypotheses (e.g., Van Valen, 1985a), where one hypothesis is given an initially privileged position. Alternatively, by treating possible causes together we are in the framework of estimation rather than hypothesis-testing (not that the latter is always unimportant) and we have an

Table 2. Amounts of selection in the late Paleocene, through 3.5 Ma.

Unweighted	Species	Genera	Families	Orders
Placentalia	0.29	0.46	0.16	0.07
Marsupialia	0	0	--	--
Multituberculata	0.21	0.08	0.13	--
combined	0.29	0.40	0.16	0.07
insectivores	0.40	0.28	0.09	0.00
all herbivores	0.24	0.52	0.22	0.14
herbivorous placentals	0.18	0.65	0.23	0.13
carnivores	0	0	0.02	0.02
among trophic groups	0.010	0.003	0.004	0.007
Weighted				
Placentalia	0.18	0.58	0.20	0.09
combined	0.22	0.48	0.21	0.10
among trophic groups	0.010	0.001	0.001	0.002
	*	*	*	*

initial predilection to ask, e.g., how much each process contributes, if anything.

### Mammals

So what does all this let us say about the Paleocene radiation of mammals? I will discuss its evolution in western North America, the only region where data even approach adequacy yet. I know these mammals, and all the information, from correlation and age to phylogeny and classification, and often even specimen identification, has filtered through me with modifications as appropriate. That doesn't mean it's right, but it does ensure some comparability; the analyses aren't based on someone's compilation of the work of others with diverse standards.

Including the terminal Cretaceous and basal Eocene, there are so far about 21 distinguishable time zones, of very unequal durations. Because taphonomic and collecting biases are not yet controlled, I have had to use species rather than individuals as the lowest unit. Damuth (1987) has shown that the largest potential source of bias for species, body size, has no effect on energy flow. The remaining variation is large but I have had to assume that all species of a single trophic group use the same amount of energy per year. For this reason and others, my results are only preliminary.

There are a number of useful ways to partition a set of contemporaneous species. I will look at two: taxonomic and trophic. Taxa are not arbitrary constructs, although their boundaries are often fuzzy with respect both to their contents and to what category includes them. It is a common fallacy to confuse reality with discreteness. Green differs from blue, youth differs from maturity, and the boundary between a species and its ancestor is rarely sharp even with punctuation. A higher taxon is an adaptively unified segment of a phylogeny.

There were large changes in mammalian faunal composition through the Paleocene, starting with a dominance of small marsupials and multituberculates in North America and ending with early members of most of the modern placental orders, with others sharing dominance in the interim. The concomitant large changes in the partitioning of energy flow are the focus of my analysis, which will estimate group selection at various levels.

All the faunal changes are presumably selectively controlled. That doesn't mean that all the change in representation of, say, two orders is a result of their ordinal characters; it may alternatively, or in addition, be a result of properties of taxa included within the orders, with the ordinal change being a byproduct.

Table 3. Numbers of different kinds of transitions in the two intervals.

	Persistence	Extinction	Branching	Phyletic evolution
Basal Paleocene (0.5 Ma)				
species	6	13	36	40
genera	14	7	20	8
Late Paleocene (3.5 Ma)				
species	35	26	13	21
genera	54	16	5	5
	*	*	*	*

Similarly, families may differentially expand as a byproduct of ordinal characters. Distinguishing these levels requires probably more information than we have about specific adaptations, many of which are undoubtedly not even preserved, like herbivore stomachs or caeca. Nevertheless, I can see no way in which change at this level can be causally random with respect to everything.

From more extensive work in progress, I will summarize some results for two intervals, the beginning of the radiation and an interval well into it. Specifically, these are early Bugcreekian to about the Mantuan-Puercan boundary and middle Tiffanian to early late Tiffanian. The first interval contains six zones (one not yet published as such) but lasted only perhaps 500,000 years; the second contains two or perhaps three zones and lasted about 3.5 million years (cf. Sloan, 1987).

An appropriate measure of selection in this context is the variance in absolute realized fitness, this fitness being the ratio of the number of descendant species (if any) to their ancestors. The variance of this fitness then measures the total amount of ostensible selection in a particular partitioning. Crow (1958) used a somewhat similar measure in a different context. Because species are vicars for energy in my analysis, they are the units used for each taxonomic category.

Even though the later interval is perhaps seven times longer, Tables 1 and 2 show that the amount of selection on placentals is a hundredth or less in the later interval for all categories from species to order. This is the case whether or not the species are weighted by their trophic class. Multituberculates began their slow extinction with the expansion of placentals, but they too show much less selection later. Herbivores were one to two orders of magnitude more selected than insectivores in the earlier interval, which was the beginning of the placental-herbivore radiation, but there is no difference between them later in the Paleocene. Selection is only partly independent among different levels and the amounts are rather similar among the levels in all comparisons.

In the later interval a much larger proportion of the species and genera persist through the interval (Table 3). Extinction is also more important then, even with the near demise of the marsupials and large groups of multituberculates earlier. Contrarily, phyletic evolution and especially the branching of lineages are both more important at the beginning of the Paleocene. No likely cases of immigration occur in the intervals discussed here, although this can rarely be excluded. Where it can be analyzed, expansion is the predominant mode of change throughout.

Predation was uniquely and remarkably weak on mammals in the early Paleocene (Van Valen, 1978). Therefore the initial organization of placental communities was presumably by competition.

There is a lot more that could be said, but we may see that this approach gives a suitable way of analyzing the changes in the partitioning of energy flow in communities and larger biotas. These changes were indeed large and rapid in the earliest part of the Paleocene. Undoubtedly a more accurate picture can be made for the Pleistocene; less has happened so far in this epoch (pending more human



destruction) in the composition of the world's biota, but the changes in partitioning of energy flow since the latest glaciation may well be as profound.

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