

Confusion Over Evolution': An Exchange

To the Editors:

There are many points in Stephen Jay Gould's curiously ill-tempered review of Helena Cronin's *The Ant and the Peacock* [NYR, November 19, 1992] that I disagree with, but I will content myself with one. Cronin argues that the apparent altruism displayed by some animals (the Ant of her title) raised a question for Darwin that he was unable fully to answer, but which has been answered by a gene-centred approach. Early in his review, Gould states that "the key question evoked by the ant's altruism has not been resolved." When I read this, I was puzzled: has Gould spotted a fallacy in the argument that I have missed? Not at all. It later turns out that Gould fully accepts Cronin's explanation of the social behaviour of ants in terms of the genetic relatedness between the members of a colony, an explanation first proposed by W.D. Hamilton. So why has the question not been resolved?

It turns out that the failure is no more than this; the gene-centred argument cannot explain human altruism, which is often directed to non-relatives. Coming from anyone this argument would be odd, but from Gould it is astonishing. For years he has been inveighing against those who regard evolution as an inevitable progress culminating in man, and emphasizing the marvellous diversity of life. Now he tells us that a biological argument fails if it cannot fully explain some feature peculiar to humans. If so, I have wasted my life, and so, for that matter, has Gould. As it happens, I agree with him that there is more to the evolution of human altruism than kin selection: once a species has acquired language as a second method of passing information between generations, new mechanisms of change become possible. But to dismiss half of Cronin's thesis on these grounds is ridiculous.

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To the Editors:

As an educator, Stephen Jay Gould has illuminated literally hundreds of dark corners of biology for us all, but he is also a formidable polemicist whose campaigns have blighted more than a few reputations and careers. There is a delicious irony, therefore, in his desperate attack on Helena Cronin's *The Ant and the Peacock*. For years he has tried to divert our attention from the "Panglossian" strategic principles of adaptationism, and now he has stubbed his own toe on one of them: if an organism has one trick that it always uses, chances are that eventually the evolving world will catch on and expose it to counter-measures. Gould's trick is refutation-by-caricature, and this time he exposes himself with stunning efficiency, even candidly admitting, at one point, that in the past he has stooped to caricature of the opposition.

Gould's basic trick, honed over the years, has a nifty second stage. In the first stage, you create the strawperson, and "refute" it (everybody knows that trick). Second (this is the stroke of genius), you yourself draw attention to the evidence that you have taken the first step—the evidence that your opponents don't in fact hold the view you have attributed to them—but interpret these citations as their grudging concessions to your attack!

The trick becomes transparent with overuse, however, and Gould has managed to epitomize his career with this ploy in the confines of a single article. Here are three distinct instances.

(1) He correctly identifies Cronin as belonging to the school of his nemesis, Richard Dawkins (hence the vituperation). He characterizes Dawkins' "genetic selectionism" as "hyper-Darwinian reductionism" and attributes to him (without citation) the view that the gene's perspective is "exclusive," which apparently means that genic selectionism is held to be "the fully comprehensive theory of biological change." But it is Gould, not Cronin or Dawkins, who makes this "strange assertion." Instead of bothering to refute this straw doctrine, Gould refers the reader to

"sharp and devastating criticism both from biologists and philosophers." Many of us who know the literature he cites would not describe it in those terms. For an accessible and trenchant antidote to Gould's overstatement, see Philip Kitcher and Kim Sterelny, "The Return of the Gene," *Journal of Philosophy*, 1988, pp. 339–361. In any event, with breathtaking *chutzpah*, he then describes Dawkins' *The Extended Phenotype* (1982) as containing a "fatal concession," a "stunning admission of relativism that flatly contradicted Dawkins' previous claim for true and exclusive causality at the genic level." So are we to believe that Dawkins admitted defeat in 1982, and Cronin, a close colleague in the same department, hasn't yet noticed, and continues to sing the song he abandoned a decade ago? Gould never quotes an instance of her commitment—or Dawkins' commitment—to the caricature he foists on them. In fact, Dawkins himself regards *The Extended Phenotype* as anything but a pulling back. He sees the book as a more radical extrapolation of the now widely accepted thesis of the selfish gene.

(2) Gould characterizes adaptationism as "pure adaptationism" and "panadaptationism"—which is apparently the view (he never defines it) that every feature of every organism is to be explained as an adaptation selected for. But Cronin herself is particularly acute in criticizing this view (pp. 66–110) and, in particular, one of Gould's earlier misconstruals:

...Stephen Gould talks about "what may be the most fundamental question in evolutionary theory" and then, significantly, spells out not one question but two: "How exclusive is natural selection as an agent of evolutionary change? Must all features of organisms be viewed as adaptations?" (Gould 1980, p. 49, my emphasis). But natural selection could be the only true begetter of adaptations without having begot all characteristics; one can hold that all adaptive characteristics are the result of natural selection without holding that all characteristics

are, indeed, adaptive. (p. 86)

I will play Gould's second card for him here, so you can see the strategy in its purest form: Don't you see? She has to admit that her panadaptationism can't explain everything!

(3) The most transparent case is Gould's invention of "extrapolationism," described as a logical extension of "Cronin's adaptationism." This is a doctrine of pan-continuity and pan-gradualism that is conveniently—indeed trivially—refuted by the fact of mass extinction. "But if mass extinctions are true breaks in continuity, if the slow building of adaptation in normal times does not extend into predicted success across mass extinction boundaries, then extrapolationism fails and adaptationism succumbs." I cannot see why any adaptationist would be so foolish as to endorse anything like "extrapolationism" in a form so "pure" as to deny the possibility or even likelihood that mass extinction would play a major role in pruning the tree of life, as Gould puts it. It has always been obvious that the most perfect dinosaur will succumb if a comet strikes its homeland with a force hundreds of times greater than all the hydrogen bombs ever made. There is not a word in Cronin's book that supports his contention that she has made this error. If Gould thinks the role of mass extinctions in evolution is relevant to either of the central problems Cronin addresses, sexual selection and altruism, he does not say how or why. When Cronin turns, in her last chapter, to a fine discussion of the central question in evolutionary theory she has not concentrated on, the origin of species, and points out that it is still an outstanding problem, Gould pounces on this as a last minute epiphany, an ironic admission of defeat for her "panadaptationism." Preposterous!

What irks Gould the most, he makes clear, is Cronin's claim that what she is describing and defending is "modern Darwinism," whereas he claims that "the main excitement in evolutionary theory during the past twenty years" has been "the documentation of the reasons why Darwin's

crucial requirement for extrapolation has failed." Gould is referring, of course, to the whipped-up brouhaha surrounding his own three false-alarm "revolutions" in Darwinism: exaptation, punctuated equilibrium, and, most recently, species selectionism.

The Ant and the Peacock is scholarly and insightful, witty and vivid without being bullying. Gould's review of it contains other mistaken objections and misrepresentations, but these three cases will do handsomely to disarm the rest.

Daniel C. Dennett

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Stephen Jay Gould replies:

In reading these two critiques, I can only perceive myself on the receiving end of a good-cop-bad-cop grilling. I therefore begin my defense by epitomizing my assessment of Helena Cronin's book: She argues that gene selectionism is the key ingredient of a major revolution (she calls it "modern Darwinism") that has reshaped our view of evolution by recognizing that genes, rather than organisms (as Darwin held), are primary units of natural selection. She symbolizes the supposed success of this revolution by the two chief problems putatively solved (sexual selection as displayed by the peacock, and altruism as illustrated by the ant). I summarized the philosophical and empirical arguments that have convinced most of my colleagues that exclusive gene selectionism is both logically and factually wrong, and I supported the hierarchical model that views selection as acting simultaneously at a variety of levels in a genealogical sequence of gene, organism, population, and species. I then argued that the ant and peacock do not support Cronin's scheme because sexual selection (the peacock) can be resolved at the conventional Darwinian level of selection on organisms, while gene selectionism, though successful in explaining many cases of animal altruism (including the ant) cannot render the distinctive human form that set the philosophical problem in the first place. Finally, in reviewing two other books by paleontological colleagues, I argued that short-term selection in populations (at any level) cannot explain major geological patterns in the history of life.

My dear colleague and good-cop John Maynard Smith (who wrote the preface to Cronin's book) only reiterates a point that I made myself (though with a markedly different slant). I allowed that gene selectionism has resolved many cases of animal altruism and I praised Cronin's consideration of this issue by writing: "I agree with Cronin up to a point, and I greatly appreciate her incisive treatment." Now, in most cases, I would concur with Maynard Smith that a claim for human difference only rep-

resents the peculiarity of an odd species, and shouldn't rain on the parade of a general evolutionary solution. But altruism falls into a different category of intrinsically human conundrums because its classical moral and philosophical focus has not been addressed by the evolutionary solution: why are humans so prone to perform acts that both benefit others and endanger themselves. The evolutionary argument holds that animals perform such altruistic acts toward relatives who share enough of their genes to render the potential sacrifice beneficial to the altruist's genetic heritage. But since most human acts of altruism are performed in the service of non-kin, this explanation cannot hold for our brand (as Maynard Smith agrees).

Within the little community of professional evolutionists (that John and I proudly call our own), the gene-selectionist account of "altruism" matters greatly, but we cannot and dare not claim that we have thereby solved the classic philosophical issue generally encompassed by this word. For we transmuted the vernacular word "altruism" to a quite different technical sense—and then solved the technical issue, leaving the human phenomenon (for which the word was invented) quite unresolved. If Cronin had only angled for the narrow technical sense, then I would have no beef; but she herself laid claim to the human prize by writing as the longest chapter in her book: "Human altruism: a natural kind?"

The less than collegial tone of Daniel Dennett's commentary affirms the worst suspicions bruited in some quarters about the pungently rarified air of Cambridge, Massachusetts. (Thank God for Fenway Park and my local Bowl-a-Drome, where these mental pirouettes can be temporarily put aside and a semblance of populist normality attained.) Really, Dan, however much you may find my views on adaptation distasteful, why do you use this forum to air your personal grievances? Nearly all your commentary treats my doubts about adaptation. But I said scarcely anything about this subject in my review of Cronin (only one column of the fifteen devoted to her book, with further comments in the last section, four columns long, that treats the two other books). My commentary centers on her advocacy of gene-selectionism—and I criticize her from a standpoint *within* selection theory by defending the hierarchical concept described above. Since I am operating within selection theory, and selection generally leads to adaptation, my critique of Cronin does not involve those aspects of my work that you dislike (i.e., my doubts about organismal panadaptationism). Moreover, I devoted most space to logical and philosophical refutations of gene selectionism (the concept of emergence and the confusion of bookkeeping with causality). You are a professional philosopher; why did you not comment upon the bulk of the review at all?

Your three points supposedly seal my malffeasances, but none of your charges hold. You say I erected a strawman in stating that Cronin views genes as the only acceptable level of selection. But she says exactly this and I quoted her argument in my review (though you deny that I so cited her!):

Genes, then, can be replicators whereas organisms, groups and other levels of the hierarchy cannot. Natural selection is about the differential survival of replicators. So genes are the only serious candidates for units of selection.

Ipsa dixit.

My review treated three books—Cronin's and two by my paleontological colleagues Peter Ward and Niles Eldredge. You accuse me of further unfairness to Cronin in the last section, which does not treat her work but discusses the good arguments of Ward and Eldredge against the extrapolationist model so vital to Darwin's own world view (the rendering of geological pattern by successive accumulation of tiny generation-by-generation increments. To cite Darwin's memorable words: "Natural selection is daily and hourly scrutinizing...every variation, even the slightest.... We see nothing of these slow changes until the hand of time has marked the long lapse of ages.") Dennett writes: "I cannot see why any adaptationist would be so foolish as to endorse anything like 'extrapolationism' in a form so 'pure' as to deny the possibility or even likelihood that mass extinction would play a major role...." But Darwin himself took just such a position in trying to identify mass extinction as an artifact of an imperfect fossil record (see "On Extinction," pp. 317-322 in the 1859 first edition of the *Origin of Species*: "we must remember... the probable wide intervals of time between our consecutive formations; and in these intervals there may have been much slow extermination").

Dennett accuses me of advancing these paleontological claims only to toot my own horn—in his words the "whipped-up brouhaha surrounding his own three false-alarm 'revolutions' in Darwinism: exaptation, punctuated equilibrium, and, most recently, species selectionism." But my paleontological arguments in the review do not mention any of these themes (which are central to my view of life). I wrote instead about the neutral theory of nucleotide evolution and of mass extinction—and I have done no research on either of these subjects (though I greatly appreciate what my colleagues have accomplished in these areas).

Dan, the letterhead of your stationery carries the motto of your university: *pax et lux*. Your unfair and unkind comments proffer precious little of the first, and therefore provide about as much of the second.

The Confusion over Evolution

Stephen Jay Gould

The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today
by Helena Cronin.
Cambridge University Press, 490 pp., \$39.50

The Miner's Canary
by Niles Eldredge.
Prentice Hall, 246 pp., \$19.50

On Methuselah's Trail: Living Fossils and the Great Extinctions
by Peter Douglas Ward.
W. H. Freeman, 212 pp., \$18.95

Oliver Cromwell delivered history's most famous rebuke to the hero-worshipping that irons all subtlety into flawless cardboard:

Mr. Lely, I desire you would use all your skill to paint my picture truly like me, and not flatter me at all; but remark all these roughnesses, pimples, warts, and everything as you see me, otherwise I will never pay a farthing for it.

Helena Cronin, in *The Ant and the Peacock*, displays a raw talent clearly equal to that of our finest portraitists, but has placed herself into a position even worse than Mr. Lely's. Cromwell's painter at least faced the subject himself; Cronin has produced an uncritical gloss upon a false and simplistic view that never was more than a caricature of Darwinian theory.

As its most deliciously radical component, Darwin's original theory proposed a causal mechanism for evolution by natural selection among organisms struggling for personal reproductive success—and nothing else. Consider the impact of this cleansing upon the older tradition of natural theology—the creationist principle that sought to prove not only God's existence, but also his attributes of power and goodness, from the excellent design of organisms and the intrinsic harmony of ecosystems. Darwin acknowledged these aspects of nature, but labeled them as sequelae, or side consequences, of the only causal force operating in evolutionary change: organisms struggling for themselves alone. Quite a contrast: up from below in the "selfish" interest of organisms vs. down from above as directly imposed by a wise creator.

Inevitably, I suppose, Darwin's success in pulling down the level of causality from an overarching God to a struggle among organisms led some evolutionists to explore a kind of ultimate reductionism in viewing genes themselves as the struggling units, and organisms as mere vehicles constructed for their machinations. Under such a view, called "gene selectionism," nature's truly causal competition takes place among different forms of a gene, each "struggling" to leave more copies of its own version in future generations of a population. In classical Darwinism, organisms struggle for reproductive success. (If, for example, short plants are favored by natural selection, then the runts in Mendel's pea patch produce more surviving off-

spring, per individual and on average, than the tall plants.) In gene selectionism, the plants are passive vehicles and the struggle occurs among genes. (If you can dredge up your high school biology, you will remember that T and t ["big t" and "little t" even in biological jargon] are different forms [called alleles] of a gene at a chromosomal position [called a locus] influencing the height of the resulting pea plants. Under gene selectionism, little t is struggling with big t to leave more copies of itself in the next generation. Selection is then viewed as working for little t alleles, not for short plants.)

Several of my colleagues toyed with this formulation during the 1970s, while Richard Dawkins provided a popular version in his book *The*

Phenotype, 1982), which opened with the fatal concession that natural selection among genes and ordinary Darwinian selection among organisms may be viewed as equally valid modes of description for the same causal phenomenon. (This stunning admission of relativism flatly contradicted Dawkins's previous claim for true and exclusive causality at the genic level.)

Helena Cronin, a philosopher by original profession, has gathered much interesting material in *The Ant and the Peacock*, but her book suffers grievously from the curious and vociferously advocated scheme that she has chosen as her vehicle of presentation. In short, she has somehow received the impression that genic selectionism has accomplished the

in species. Entities at each level of the hierarchy can act as biological "individuals," and Darwin's process of selection can therefore occur at all levels, with none dominant in all situations. Genes may "struggle" for increased representation in the gene pool of a population, but species may also "struggle" for increased membership of their branches in the "species pool" of an evolutionary lineage.

But whatever one's personal inclinations, no one can deny the sociological fact that relatively few experts accept the theory of near exclusivity for gene selection, and no amount of blithe verbal assurance about the validity of the theory can convert it into a successful revolution. Most of my colleagues continue to defend Darwin's view that selection works nearly exclusively on organisms.

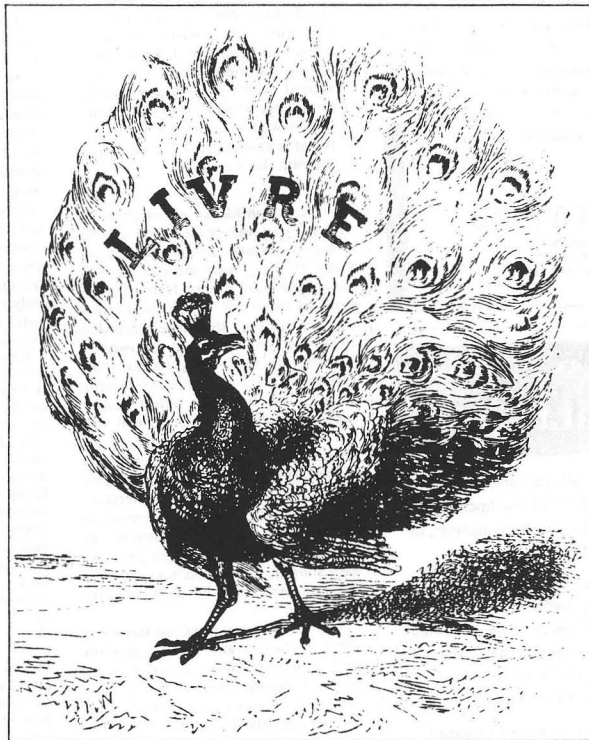
For Cronin, ants and peacocks are synecdoches for two great issues mentioned in her subtitle—altruism, epitomized by the behavior of ants in their communities, and sexual selection, the alleged *raison d'être* of the peacock's flamboyant and burdensome tail. In Cronin's view both altruism and sexual selection are explained by the theory of selfish genes; and I agree that the gene's perspective has been useful in dealing with these two substantial problems. But I shall argue that the peacock only needed classical Darwinism to account for its tail, while the key question evoked by the ant's altruism has not been resolved. If the approach of gene selectionism is false, then Cronin's title makes little sense and all her fascinating flowers of insight (primarily on the differences between Darwin and Wallace) languish in barren soil.

This attempt to validate gene selectionism by applying it to ants and peacocks fails for three main reasons (which I consider in turn in the rest of this review): 1) the general theory is bankrupt; 2) the two chosen examples form a false and disparate pairing that either does not need or does not fully illustrate the theory; 3) the theory, even if valid in its own limited realm (which it is not), cannot serve as a paradigm for all, or even much, that evolutionary theory must explain. The fine books of Ward and Eldredge illustrate why this is so.

Fallacy of the General Theory

Since Darwinism is a theory about differential reproductive success ("survival of the fittest" in the old cliché of limited utility), and since organisms are plainly doing the struggling and reproducing "out there" in nature, why would anyone want to relocate the action at the level of genes encased within these organisms? This question engages a central issue in Darwinian theory: On what kind of object does natural selection work? What, in short, is a "unit of selection"? Cronin gives her answer in no uncertain terms:

So when is an "adaptive unit" really an adaptive unit? When is a category that's seen by us, seen by nature, too? The answer must be:



Selfish Gene (1976). This hyper-Darwinian reductionism (and pervasive adaptationism, though from the gene's point of view) contained some interesting ideas and made a stir within the field. But gene selectionism—as a hard causal claim rather than a colorful metaphor—also received sharp and devastating criticism both from biologists and philosophers.¹ Even Richard Dawkins backed away in his next book (*The Extended*
¹See especially E. Sober's *The Nature of Selection* (MIT Press, 1984), E. Sober and R. C. Lewontin, "Artifact, Cause and Genic Selection," *Philosophy of Science*, Vol. 49, pp. 157–180; E. Lloyd, *The Structure and Confirmation of Evolutionary Theory* (Greenwood Press, 1988); and P. Godfrey-Smith and R. C. Lewontin's forthcoming "The Dimensions of Selection," *Philosophy of Science*.

greatest revolution since Darwin and has swept away all opposition within the field (she proclaims "revolution" as often as Marx or Thomas Kuhn, and labels the new orthodoxy "modern Darwinism").

Now I freely confess my own strong preference for the other side of this debate—for a model that views selection as operating simultaneously at several levels of a genealogical hierarchy including genes, organisms, local populations, and species. In other words, I argue that no natural entity can properly be described as the exclusive "unit of selection"—as Cronin and Dawkins would claim for genes, and classical Darwinians for organisms. Nature is organized as a hierarchy—genes in organisms, organisms in populations, and populations

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When it's a unit that selection can work on. For classical Darwinism this would have been difficult to specify precisely. But for modern Darwinism, a unit is obviously a gene and the ramifying tree of all its phenotypic effects [by "phenotypic effects," she means the manifest characteristics of the organism including its anatomy, etc.].

But if gene selectionism is so self-evidently true, why hasn't it swept the field, smiting all opposition before it? In a remarkable passage, Cronin admits the stubborn persistence of alternative interpretations, but brands them as obtuse because she so clearly grasps the true logic of genuine Darwinism—and it says what she says it says, period.

Let me forestall the mutterings of disagreement that can already be heard in the background. By no means all modern Darwinians would accept my characterisation. But I am dealing with the theory, not with how individuals have chosen to interpret it. One must distinguish between the fundamental tenets of a theory (what the theory actually says) and how it is viewed by some practitioners (what is said about it). I am dealing with the former.

Cronin's confidence arises from her misuse of an important distinction between "replicators" and "interactors" made by the philosopher of science David Hull and others. Natural selection is a theory of "differential reproductive success"; therefore, according to one school of thought followed by Cronin, only natural objects that replicate themselves faithfully can be units of selection. For if an object doesn't replicate itself faithfully, then it cannot be a reliable transmitter of the characteristics that make for superior reproductive success. Now an organism, the traditional "unit of selection" in Darwinism, fails by this criterion because, in sexual reproduction, offspring contain only half the genes of each parent. What good is a replicator that dilutes itself by half in each generation?

The genes themselves, on the other hand, replicate faithfully (except for rare mutation) into future generations. A fecund organism is passing copies of its genes, not its body, into the next generation. Under this view, genes are replicators, while bodies are, in a sense, their servants. Bodies interact with the environment and engage in the "struggle for existence" via differential reproductive success. Bodies are interactors (Richard Dawkins prefers the more loaded and almost pejorative term "vehicles"); genes are replicators. Therefore, only genes are units of selection. Cronin remarks,

Genes, then, can be replicators whereas organisms, groups and other levels of the hierarchy cannot. Natural selection is about the differential survival of replicators. So genes are the only serious candidates for units of selection.

This superficially attractive argument collapses from two major fallacies. First, it is simply not true that only genes replicate with adequate

faithfulness. I accept the point that sexual reproduction dilutes the integrity of organisms in replication. But adequate replication returns at higher levels of the hierarchy—populations and species—because splitting at these levels is analogous to asexual reproduction. For example, species split into daughter species that resemble their parental populations far more than any other (descendant dogs are more like ancestral wolves than like any other species). Species are therefore good replicators, and some evolutionary lineages can be more successful than others because their species give rise to more successful branches.

Second, the replicator criterion is at best insufficient, and at worst entirely mistaken. A simple appeal to vernacular usage tells us that a lower unit (a gene, for example) can't be an exclusive agent if all the action occurs at higher levels (organisms, for example)—and the properties that generate this action are "emergent" characters of the higher level—that is, not a simple summation of features built by the lower units (genes).² Now, manifestly (and gene selectionists do not deny this), organisms are primary objects struggling for reproductive success in nature. How, then, can "hidden" genes be the true agents if organisms are doing the fighting, cooperating, generating, and dying? Gene selectionists respond that all the relevant properties of organisms can be described as results of the various genes involved in their construction. Such properties, the argument continues, are therefore only the complex manifestation of genetic action.

²"Emergence" is a complex and contentious subject, with a long pedigree, in both the philosophical and biological literature. I use the term here in the narrow technical (virtually statistical) sense. A feature is emergent at any level if its construction requires nonadditive interaction among the factors and components that build it. In other words, if I can make a larger-scale entity D by just adding components A, B, and C together, then nothing about D is emergent—and D can be explained by reduction to its components. But if the building of D requires interactions among A, B, and C that are not inherent in the components considered separately, and cannot be predicted from knowing A, B, and C alone, then D has emergent features and cannot be explained by reduction to its component parts. Organisms clearly have emergent properties, since their features of anatomy, physiology, and behavior are products of complex and nonadditive genetic and environmental interactions—and not the summation of genes considered separately. Therefore, selection operating on organisms cannot be reduced to selection upon genes, and the "gene selectionism" of Cronin's self-proclaimed "modern Darwinism" fails.

Incidentally, the concept of emergence helps us to understand why the nature-nurture issue is such a false dichotomy. Genes influence many aspects of human behavior, but we cannot say that such behavior is caused by genes in any direct way. We cannot even claim that a given behavior is, say, 40 percent genetic and 60 percent environmental, and thereby defend at least a partial old-fashioned genetic determinism. Genes and environment interact in a nonadditive way, yielding emergent features in the resulting anatomies, physiologies, and behaviors.

But many, or most, of the summations of genes are not genes. The actions among them they cannot, or at least not at the level of genes, such as epigenetics, genes can be selected.

Moreover, frequently at an organizational level, genes give rise to an archy—on a "give" level, organisms (Diverse" level), or on species. (evolutionary) mine the re complex inter Claims for of one chose blinking.

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Review

But many, undoubtedly most, prop-
erties of organisms are not simple
summations of contributions from sev-
eral genes. They are products of inter-
actions among genes and therefore
they cannot, in principle, be ade-
quately predicted or known at the
level of genes. Since selection acts on
such emergent properties of organ-
isms, genes cannot be exclusive units
of selection.

Moreover, emergence occurs fre-
quently at all levels of biological
organization. Selection acts simulta-
neously on all levels of nature's hier-
archy—on genes (Cronin's "exclu-
sive" level), on cell lineages, on
organisms (Darwin's "nearly exclu-
sive" level), on local populations, and
on species. Our intellectual task as
evolutionary biologists is to deter-
mine the relative importance and
complex interactions of these levels.
Claims for theoretical exclusivity
of one chosen level are false and
blinkering.

Why have some scientists been at-
tracted to exclusive gene selectionism
in the light of these criticisms? I be-
lieve that the appeal of the idea rests
upon a central fallacy, one embraced
by Cronin: the confusion of book-
keeping with causality. Gene selec-
tionists have correctly noted, but
fundamentally misinterpreted, an im-
portant property of evolving systems:
all evolution by selection, whatever
its level of causation, is recorded by
change in the frequencies of genes
(the lowest level of the causal hierar-
chy). Since genes record all changes,
some evolutionists have been fooled
into assuming that genes therefore
cause all changes. But scribes are not
agents, and bookkeeping is not
causality.

This recording of all change by
genes reflects a general property of hi-
erarchies, not a statement about the
locus of causality. Disturb a hierarchy
at any level, and all units at that level
and below must be shuffled—while
higher-level units may be unaffected.
For example, suppose that the lineage
of cats once contained two groups of
five species each. They compete en-
tirely at the level of species selection
and, 10 million years later, all species
in group A are eliminated, while group
B has flourished and now contains fif-
teen species. The genetic makeup of
the entire lineage has altered as a re-
sult (for species in group A had differ-
ent genes in different proportions
from species in group B)—but no
causal process has operated at the
gene level.

But the obverse does not hold:
lower-level impacts on genes need not
affect higher-level units at all. For ex-
ample, some genes may increase their
number of copies within organisms by
gene selection alone—but organisms
need not "notice" and need not be af-
fected in any way.³ Now this asymme-

³The best example of legitimate gene
selection may be provided by a phe-
nomenon known as "selfish DNA."
Some genes can make copies of them-
selves, and these copies may then
move to other locations among the
chromosomes (so-called transposons,
or "jumping genes"). This process
constitutes positive selection for these
genes at their own level, since the
process augments the number of
copies of these genes among the

try in hierarchies—upper-level distur-
bances felt at all lower levels, but
lower-level impacts potentially invis-
ible to higher-level units—makes the
lowest level an attractive place for
bookkeeping, because all changes,
whatever their causal locus, are
recorded there.

Bookkeepers are slighted in our
metaphors as mere scribes and
recorders of action occurring else-
where. What magnificent revenge the
error of gene selectionism must
promise them! For their ledgers—the
tables of changes in genetic composi-
tion—have been misread by gene se-
lectionists as the fundamental cause of
life's history. But revenge based on
error is both short and ultimately fru-
strating, for the deprecatory metaphor
turns out to be true in this case.

*Fallacies of Cronin's Particular
Arguments*

Cronin's entire book promotes what I
like to call the Senator Aiken strategy
for untenable positions. This fine leg-
islator once proposed a wonderfully
simple solution for the morass of our
military involvement in Vietnam: Why
don't we simply declare victory and
get out! Cronin does much the same.
She proclaims victory, dogmatically
and vociferously, over and over again,
for the gene-selectionist version of
strict adaptationism ("modern Dar-
winism" in her neologism). In one re-
markable passage she even tells us
that Darwinism has triumphed on
other unknown planets because evolu-
tion can work in no other way!

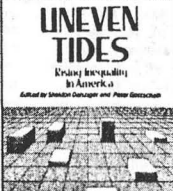
We have seen why Darwinism was
in 1859, and still is, the best expla-
nation of why living things are as
they are—not only, it turns out,
on this planet, but in any world
that resembles ours in several fun-
damental respects.

In essence, Aiken's strategy must
mask failure with a claim for triumph.
How then does Cronin manage to de-
fend such a flawed and discredited ap-
proach as pure adaptationism from the
gene's point of view? She snatches
rhetorical victory from the jaws of de-
feat by a series of false arguments and
uncritical assertions. I give examples
in just a few categories:

1) False or misleadingly incomplete
citation of empirical data. To support
her panadaptationist world view, the
belief that virtually all heritable
changes in organisms are the result of
adaptation, Cronin tells several classi-
cal tales of natural history as triumphs
of selection (when the actual story is
far more complex and ambiguous).
For example, she cites color banding
in the land snail *Cepaea* as "just one
example of natural selection rescuing
phenomena from the explanatory


chromosomes of an individual—just
as ordinary Darwinian selection on or-
ganisms increases the number of off-
spring of favored individuals within a
population. But the organism need not
"notice" as the copies of selfish DNA
increase, for these additional copies
are often without function. In fact,
gene selection can be most effective
when organisms do not "notice" the
increase—for if the increase of genetic
copies impedes the organism in any
way, negative selection from the ordi-
nary Darwinian level of organisms
may bring the process to a halt.

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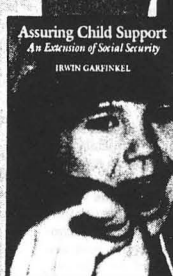
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clutches of genetic drift."⁴ (Genetic drift refers to a random process of increase or decrease in the frequencies of genes in populations. Suppose that only ten individuals exist in a species of beetles, and that three of them carry a favorable gene subject to positive Darwinian selection. An elephant rambles by and squashes half the beetles, including [by chance] all three with the favorable gene [which is now randomly eliminated from the population, despite its Darwinian value].)

Now A.J. Cain and others demonstrated the power of selection (based on visual discrimination among differently banded snails by predatory birds in different habitats) where drift had previously been assumed—and this work was a genuine triumph for Darwinism. But Cronin never mentions the second chapter of this story—Cain's unsuccessful attempts to explain so-called area effects (abrupt changes in banding types from one region to another, but correlated with no evident change in habitat) by selection based upon "cryptic environmental differences." Most snail workers (I am one) now regard area effects as nonadaptive vestiges of former historical movements of populations and habitats.⁵

2) Relegation of powerful and important exceptions to peripheries. Cronin admits the vital principle that "some side effects of adaptations, which become positively useful when

⁴Cronin gives away her biases (and any pretense of balanced argument) in such rhetorical flourishes. Why is genetic drift an "explanatory clutch"? The phenomenon is perfectly respectable and powerful, if not entirely applicable to *Cepaea*. In other give-away passages, we learn that "non-adaptive explanations cannot be treated as other than a last resort." (Why? They are also permissible in theory and robustly present in nature.) When Darwin strays from the selectionist straight and narrow, his words "need to be interpreted more generously" so that our chief icon may continue to spearhead the strict and uncompromising version of his theory. (Again, why? Darwin was not a pure selectionist.) When Wallace departs from selectionist principles, "he has a lot to answer for." (But what is his sin?) We learn that Darwin "lets us down" when he proposes group selection for human moral conduct (a proper exception to his general orthodoxy of selection on organisms). When, among the founders of population geneticists, Fisher and Haldane make some invalid statements about group selection, they are excused because they were true Darwinians at heart. But when Sewall Wright, third member of the trinity, speaks in the same vein, he is not exonerated, for he truly believed in a form of group selection. Cronin writes: "I did not include the other major founding father of modern Darwinism, Sewall Wright, among the honorable exceptions." (Now Cronin, Dawkins, and me, bundled all together, couldn't fill Sewall Wright's left pocket insofar as intellectual power is concerned—and it is simply unseemly for any of us to speak of his views in terms of honor or dishonor.)

⁵See S.J. Gould and D.S. Woodruff in "History as a Cause of Area Effects: An Illustration from *Cerion* on Great Inagua, Bahamas," *Biological Journal of the Linnean Society*, 1990, Vol. 40, pp. 67-98.

conditions change, are until then just lying around dormant." But she cautions against overuse of this principle: "Such arguments, unless they are applied with discrimination, could end up peppering the world with a multitude of characteristics that have no Darwinian purpose (even though they eventually get put to good use)." But the world is so peppered—and this seasoning is a fundamental (and non-adaptive) feature of evolution. In fact, Cronin actually admits the primary example in the very next sentence—features in the human brain, arising as nonadaptive sequelae of its computing power, as in our ability to read and write—and then buries the subject without further commentary.

3) Mis-citation of critics. Cronin quotes a line from me, for example, and delights in her discovery: "If we are programmed to be what we are, then these traits are ineluctable. We may, at best, channel them, but we cannot change them, either by will, education, or culture." She then makes the following sarcastic comment, assuming that these words, from an article I wrote in 1978, represent my own view. "That's die-hard intransigence for you! But, actually, those quotes come not from some ardent proponent of an all-in-our-genes view but from Stephen Gould, a voluble critic of selfish-gene-ery in general and of its application to humans in particular." I will admit to writing with less than optimal clarity on occasion, but there can't be much doubt that in this passage I was characterizing my opponents' views, not my own. Earlier, in the very paragraph Cronin quotes, I labeled this view as "a crude biological determinism." Of course the words convey "die-hard intransigence"—for they are my description, my caricature I will even admit, of the opposition.

4) Ignoring opponents. As I have noted, the pure gene selectionism championed by Cronin is a marginal position among evolutionists (this, of course, doesn't make it wrong). Yet Cronin falsely depicts this view as a consensus. She performs this astonishing turnabout by simply not discussing, usually not even mentioning at all, the numerous and devastatingly effective critiques that invalidated gene selectionism after its brief run of incipient popularity in the 1970s (see my first footnote).

If Cronin's general account of gene selectionism is so awry, then the chosen examples (ant and peacock), and attendant problems (altruism and sexual selection), don't fit together either, for even well-crafted pictures may jar when juxtaposed in a single frame. She claims that both are classical problems of old-style Darwinism (selection on organisms), now triumphantly solved by the modern gene-selectionist version.

In epitome, the peacock's tale (also tail) is a story of delayed vindication for selectionism. Darwin developed an ancillary mechanism, which he called "sexual selection," to explain competition among members of the same species for access to reproduction, in contrast with the usual form of "natural selection," or competition for limited resources to sustain life. (Darwin developed the term and concept in *The Origin of Species* [1859], but covered the subject most thoroughly

in his 1871 treatise on *The Descent of Man and Selection in Relation to Sex*—a work often read only for its short and speculative thoughts on human evolution, but, in the main, a long and copiously documented treatise on sexual selection throughout the animal kingdom.)

Darwin delineated two modes of sexual selection, called "male competition" and "female choice." In male competition—e.g., among antlered deer—males fight like hell and the winners get the females. In female choice males strut and preen, display and bellow, and females choose to mate with the individuals that impress them most. Peacocks, in other words, do not evolve their showy tails for direct victory in battle over other males, but to win a beauty contest run by females.

Male competition never sparked any controversy, for it looks so much like good old natural selection. What does it matter if two male deer fight for access to food or to females? They still need good weapons and nature remains red in tooth and claw. (I usually avoid this clichéd line from *In Memoriam*; but 1992 is the one hundredth anniversary of Tennyson's death, so I make an exception.) Female choice, however, elicited a firestorm of criticism. Most of Darwin's contemporaries rejected the concept, often vehemently. It was similarly ignored, and curiously so, throughout the early excitement in twentieth-century studies of animal behavior. Neither Julian Huxley nor the German ethologists had any use for the idea. But female choice has roared back to acceptability and prominence during the past twenty years—and I certainly agree with Cronin that this reversion to Darwin's original concept represents one of the most important contemporary themes in evolutionary theory.

But I strongly disagree that gene selectionism lies behind this renaissance; hence, this half of Cronin's book, while full of insight and interesting documentation, does not support or illustrate her argument. I think that she has fallen into the classic error of equating correlation with causality. It is true that gene selectionism had its fling in the 1970s and that sexual selection began its renaissance at the same time. But, during the same years, Watergate unfolded and *The Godfather* won an Academy Award—and I really don't think that these coincident events are causally related either.

You don't need gene selectionism to validate female choice; plain old Darwinian selection on organisms works perfectly well (as Darwin himself recognized in establishing the concept); females, in choosing the most healthy and vigorous males, are bolstering their personal reproductive success—the essence of the Darwinian game.

If female choice did not need gene selectionism, then why did its vindication occur so recently? When this interesting history is sorted out, I believe that the record will show a renaissance based primarily on the removal of two longstanding impediments (both mentioned by Cronin, but treated as incidental), rather than the emergence of any new (and ultimately fallacious) theory such as gene selectionism.

Disrespect for the cognitive capacity

of nonhuman animals is an impediment: Male "do-in" what female choice is a mental step that cognitive ability to humans: that they a field ar

on some ae; in sight or weren't willing to animals. Now the insight was an unwillingness the driver's s change. Again, represents the control, but females go to adornment and await the judge nearly every sci ology was also serve until this have to be an act male choice in s world. You ma on earth and st and intellect doesn't include in such control the source of bl line cited by British biologist nent St. George "Such is the in feminine capric coloration coul selective action.

I don't mean to piece of content rectness, but in acceptability formulated con lies in the social ism and species this concept's nence largely a political questio well as the tary sociolo ence: the entr into the profess

If the peac Cronin's choser tionism because deed been solve particular appr the ant (altruis for the ant doe has not been s social insects p though genetic: the "soldiers" and hills. But evolve if the Da mentally about success? (Evol fine altruism in tional sense as h one's own rep the service of r worker ants m example, but a with other case an altruist for others—warni who sight a p Thus, the prob fined, has been theory.)

On this issue, to a point, and incisive treatm problem of alt greatest success

Descent of relation to only for its thoughts on the main, a noted throughout the modes of male competition. In male antlered and the female display choose to impress her words, males for diher males, st run by sparked so much. What deer fight? They nature re- (I usually In Memo-hundredth death, so I le choice, m of criti-mpo- n ve-ored, and e early ex-ary studies ner Julian thologists but female acceptabil- the past nly agree on to Dar-resents one temporary ty. at gene se-naissance; ook, while ing docu- t or illus- at she has equating It is true its fling in selection ame time. Watergate r won an ally don't events are tionism to old Dar-ns works mself rec-cept): st healthy bolstering success— a game. need gene d its vin- when this I be- a re- on the g impedi-ronin, but her than (and ulti- has gene e capacity

of nonhuman animals formed the first impediment: Male competition is just "doin' what comes naturally," but female choice requires an additional mental step that seemed too close to cognitive abilities supposedly unique to humans: that is, females must survey a field and make a judgment based on some aesthetic criterion of beauty in sight or sound. Most biologists weren't willing to grant such capacity to animals. Now we know better, but the insight was a long time coming.

The second impediment arose from an unwillingness to place females in the driver's seat of evolutionary change. Again, male competition just represents the big boys in ordinary control, but female choice argues that males go to enormous lengths of adornment and posturing—all to await the judgment of females. Like nearly every science, evolutionary biology was almost entirely a male preserve until this generation. You don't have to be an active sexist to ignore female choice in such a male-dominated world. You may be the kindest male on earth and still fall prey to a social and intellectual atmosphere that doesn't include the concept of females in such control. (Sometimes, however, the source of bias is more overt. In a line cited by Cronin, the prominent British biologist and Darwinian opponent St. George Mivart proclaimed: "Such is the instability of a vicious feminine caprice, that no constancy of coloration could be produced by its selective action.")

I don't mean to sound like a mouth-piece of contemporary political correctness, but I do feel that the delay in acceptability for Darwin's well-formulated concept of female choice lies in the social impediments of sexism and speciesism. And I suspect that this concept's recent rise to prominence largely reflects the social and political questioning of such biases, as well as the most important and salutary sociological shift in recent science: the entrance of so many women into the profession.

If the peacock doesn't fit into Cronin's chosen setting of gene selectionism because the problem has indeed been solved, although not by her particular approach, then the issue of the ant (altruism) is quite different—for the ant does fit, but the problem has not been solved. Ants and other social insects produce mostly sterile, though genetically female, offspring—the "soldiers" and "workers" of hives and hills. But how can such sterility evolve if the Darwinian game is fundamentally about *personal* reproductive success? (Evolutionary biologists define altruism in this limited and operational sense as behavior that decreases one's own reproductive potential in the service of others. The sterility of worker ants may represent an extreme example, but animal behavior is rife with other cases that merely endanger an altruist for the apparent benefit of others—warning calls issued by birds who sight a predator, for example. Thus, the problem of altruism, so defined, has been central in Darwinian theory.)

On this issue, I agree with Cronin up to a point, and I greatly appreciate her incisive treatment. A solution to the problem of altruism has provided the greatest success for viewing evolution

from the gene's point of view, while directly departing from Darwin's own focus on organisms. The key insight, usually called "kin selection theory," was provided by W.D. Hamilton in the mid-1960s, though many hints and half-formulations can be found in earlier literature.

What is the "individual reproductive success" of which Darwin speaks? It cannot be the passage of one's body into the next generation—for, truly, you can't take it with you in this sense above all! "Reproductive success" can only mean the passage of more copies of one's own genes into future generations. Such success is usually best achieved by bearing a maximal number of surviving offspring oneself—hence the usual Darwinian struggle for personal reproduction. Usually, but

not always. We share, on average, a certain percentage of genes with our relatives, depending on closeness—one half with each of our parents and full sibs, one fourth with our grandchildren and half-sibs, one eighth with our first cousins.

Now suppose that I am in a position where I can either die to save three full sibs or survive at the cost of their death. What should I do in the Darwinian calculus? Die for the three sibs, of course, for they represent, in sum, 150 percent of my genes, while I hold only 100 percent. Better for my genes if I go in order to let three of them live to reproduce. My act may look altruistic from the organism's point of view, but it is properly selfish and Darwinian from the gene's perspective. In short, the theory of kin selection ex-

plains apparent acts of sacrifice as evolved Darwinian adaptations in the cardinal interest of passing more copies of one's genes to future generations.

The model is powerful because it suggests an eminently testable research program: study the context of altruistic acts and see if they are performed for the benefit of enough close relatives to overbalance, through fecundity of kin, any individual loss of reproductive success. The model has been tested and confirmed in a wide variety of cases, including sterility in social insects—as among ants, where the sterile females known as workers forgo their own reproduction to help their mother, the queen, raise fertile sisters.

But we now come to the crucial, if

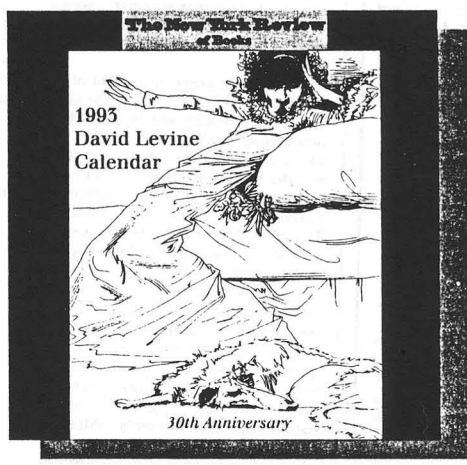
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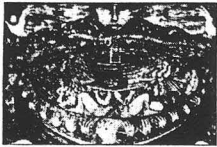
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admittedly parochial, limit. We are primarily interested in the problem of altruism because human beings seem so singularly capable of behavior in the apparent interest of others. Manifestly, this behavior is frequently not directed toward close relatives (especially since we don't choose to describe sacrificial acts between parents and children as altruistic)—and therefore can't be encompassed by the gene-centered argument of kin selection. Biologists may choose an operational redefinition of the vernacular word "altruism" as apparent sacrifice for actual genetic good, but this concept does not apply to most human acts deserving the word (and one might even argue that the vernacular notion demands no hidden selfishness at any level).

One might reply that the introduction of vernacular human altruism into the argument is unfair. After all, if gene selectionism has been successful for ants and other animals, then grant the victory and leave us out of it (for the professional enlightenment would still be great, even if the subject then failed to touch popular interest in our own condition). But Protagoras was apparently right (even if he only spoke for half of us) when he proclaimed that "man is the measure of all things," and few writers for general audiences can resist the temptation of trying to extend their perspective to this greatest prize of all. The longest chapter in Cronin's book is titled: "Human altruism: A natural kind?"

How then might the acknowledged success of gene selectionism be useful to us in understanding human altruism? Several approaches have been tried, and none have succeeded. One might argue, as Robert Trivers and others have, that the calculus of kin selection won't work, but that a different kind of selfish and adaptive advantage arises through the old principle of "favor banking." If I am perceived as a good altruist through acts that help nonrelatives, then other people are more likely to help me when I am in need—so called "reciprocal altruism." Fine, but we scarcely need Darwinism, or genetic arguments at all, to convince us that humans are smart enough to figure out the advantages of "you scratch my back and I'll scratch yours."

Or we might argue, as Cronin often suggests, that our general altruistic urges evolved long ago by kin selection among small groups of relatives, where neighbors were invariably kin, and the evolutionary rule of "be nice to those close by" would suffice to guarantee the Darwinian calculus. True altruism to nonrelatives would then be a consequence of formerly advantageous behavior, now altered by a changing social setting that makes neighbors of genetic strangers. I find this argument unattractive on two grounds. It is, first of all, an untestable speculation about unrecoverable behavior patterns of distant ancestors. Second, historical origin and current status represent entirely different problems in evolutionary biology. So what if the historical origin of altruism were adaptive via kin selection? If we still do it, after centuries of contexts unfavorable to the Darwinian calculus, then altruism is a currently non-adaptive behavior (in the narrow Dar-

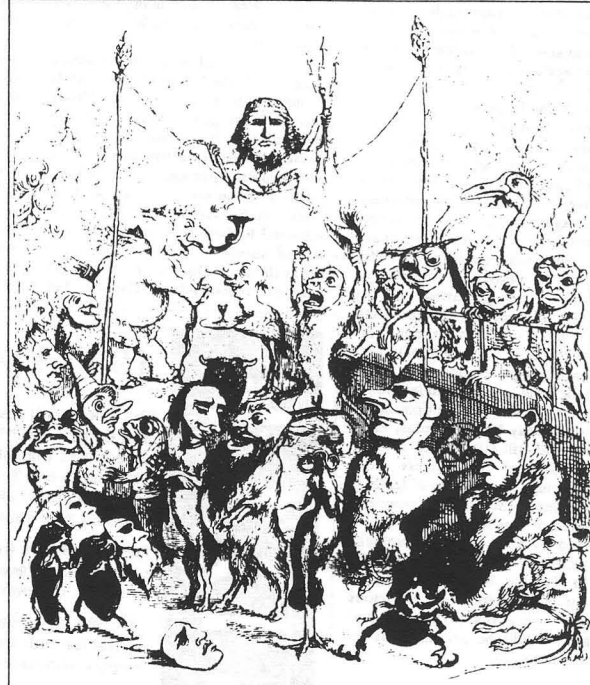
winian sense) demanding some other explanation, presumably social rather than directly biological.

In sum, the ant and the peacock are apples and oranges. Gene selectionism neither unites the problems nor resolves the issue. We don't require gene selection for the peacock, for Darwin resolved this problem within his system of selection on organisms, though we needed another century to dissolve social barriers impeding the acceptance of his answer. Gene selectionism has been useful in explaining many examples of what we call "altruism" in nonhuman animals (including ants), but it cannot resolve the vernacular human style that remains our ethical glory and our intellectual burden. The ant and the peacock don't belong together, and Cronin's book is incoherent (in the literal, not the pejora-

tic form, and the flawed inference that this supposed domination provides, by extension, an adequate account of evolution at all scales.

I have argued that gene selectionism is an ultimately incorrect view of evolutionary mechanics. But suppose it were right. Would gene selectionism then be the fully comprehensive theory of biological change that its advocates tout so vociferously? As a paleontologist, working with changes in units of millions of years rather than generations, I find this strange assertion to be the most blinkered and untenable in the entire catalog of strict Darwinian parochialisms.

Darwin himself relied crucially on such an extrapolative vision: smoothly extend the adaptive struggles of generations across millions of years in geological time, and you will obtain the



entire, wondrously ramified tree of life. Consider two famous passages from the *Origin of Species*:

*The Strictly Limited Domain of
Adaptationism, Whether Gene
or Organism Based*

In praising the power of selection, Cronin writes:

The general point has been to illustrate how resourceful and subtle a tactician natural selection can be... Once this is appreciated, non-adaptive explanations cannot be treated as other than a last resort. And resolute adaptationists can be confident that "The use of each trifling detail of structure is far from a barren search to those who believe in natural selection." [The last line is a quotation from Darwin's 1862 book on orchids.]

Such confident effusions exemplify two crucial errors: the false claim that selection dominates the domain of or-

ganism, and the flawed inference that this supposed domination provides, by extension, an adequate account of evolution at all scales.

It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whatever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress until the hand of time has marked the long lapse of ages.

The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, in so far, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many paleontologists, that organization on the whole has progressed.

If this un-

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If this uniformitarian vision of extrapolation fails, then we must conclude that while adaptationism may control immediate changes in the overt forms of organisms, it cannot render evolution at other scales. The main excitement in evolutionary theory during the past twenty years has not been—as Cronin would have us believe—the shoring up of Darwinism in its limited realm (by gene selectionism or any other patching device), but rather the documentation of the reasons why Darwin's crucial requirement for extrapolation has failed. Selectionism is not a general model for evolutionary change at most scales.

In the world below organisms, at the scale of changes in nucleotides of the DNA code, Motoo Kimura's theory of neutralism (based on the prevalence of genetic drift, as defined earlier), combined with a better understanding of genetic mechanisms, has demonstrated the neutrality of much, if not most, alteration at minimal magnitude. Selectionists often respond, as Cronin does, that their Darwinian preferences are not thereby compromised because such neutral genetic changes do not alter the external forms of organisms, and therefore couldn't be "seen" by natural selection anyway. Cronin writes: "[Kimura's] theory also assumes that chance is an evolutionary force but it is to do with changes at the molecular level that have no phenotypic effects, not evolution in the sense that we are concerned with—adaptive change." But how can you dismiss a process that probably accounts for more than 50 percent of all genetic change by noting that such alterations don't manifest themselves at the level that happens to interest you most? This special interest, after all, is just a parochialism based on human sizes and lifetimes, and on the history of our thinking. Nature, working at so many other scales, takes scant notice and plays no favorites. If we lived in the world of nucleotides, we would see the random ebb and flux as fundamental and view occasional islands of adaptive coagulation at larger scales as peculiar exceptions in an alien domain.

But the ultimate failure of Cronin's adaptationism, as a general evolutionary model, appears most clearly when we consider the paleontological record. Darwin's vision may prevail in the here and now of immediate adaptive struggles. But if we cannot extend the small changes thereby produced into the grandeur of geological time to yield the full tree of life, then Darwin's domain is a limited corner of evolutionary explanation. New documentation on the rapidity and intensity of mass extinction (including the event that wiped out dinosaurs) has provided the strongest argument for rejecting Darwinian extrapolation. Darwin clearly understood the threat, and he struggled against the implications of mass extinction in the *Origin of Species* by trying to deny both their extent and rapidity. He endeavored to spread them out in time and diminish their effects. He attempted to render them as an intensification of ordinary competition (inspired, perhaps, by an increase in rates of change for conventional processes like mountain-building and change in sea level). But if mass extinctions are true breaks in

continuity, if the slow building of adaptation in normal times does not extend into predicted success across mass extinction boundaries, then extrapolationism fails and adaptationism succumbs.

The Permian extinction (about 225 million years ago) may have wiped out 95 percent of marine invertebrate species. The Cretaceous extinction (about 65 million years ago) was probably set off by the impact of a large extraterrestrial body. The adaptive struggles of millions of previous years, whatever their intensity and the beauty of their results, could not prepare organisms for a random catastrophe. A fish honed to hydrodynamic perfection will still die if the pond dries up. Survival through mass extinction requires the good luck of evolving features for one reason in normal times, and then finding them fortuitously well-suited for survival through unanticipated catastrophe.

Two of my colleagues, Peter Ward and Niles Eldredge, have recently written short and incisive books on mass extinction. Taken together, this pair provides a fine documentation for why Darwinian selection cannot, by extrapolation, encompass the history of life. The books differ greatly in both content and intent. Ward's *On Methuselah's Trail* is a personal account of the fieldwork that convinced him about the catastrophic character of mass extinctions, particularly the event that occurred at the end of the Cretaceous period. Eldredge's *The Miner's Canary* strongly doubts scenarios of extraterrestrial impact and focuses on similarities between mass dyings of the past and the current human assault upon biodiversity (hence the metaphorical title, invoking the organic side of our chief industrial symbol for harbingers of death by environmental poisoning). Both books recognize the special and dominant character of mass extinctions as agents that changed the pattern of the history of life.

Consider just one example, supreme in its parochial importance—for I wouldn't be writing and you wouldn't be reading otherwise. Why did mammals survive, but dinosaurs die, in the great Cretaceous extinction, an event almost surely triggered by extraterrestrial impact? The adaptationist and extrapolationist model strives to render such a turnover as intensification of a process already underway in previous normal times—the growing domination of mammals as a result of their success in ordinary Darwinian competition against inferior dinosaurs. But such a comfortable argument cannot hold. Mammals emerged at about the same time as dinosaurs. Mammals lived for more than 100 million years in the interstices of a world dominated by much larger dinosaurs; they made no "progress" against these massive incumbents; no Mesozoic mammal was much larger than a rat. (By contrast, the so-called "age of mammals" since the death of dinosaurs has so far spanned only 65 million years.) The Cretaceous catastrophe removed dinosaurs, but mammals survived and inherited an emptied world—and they surely made the most of it.

If the comet or asteroid had not struck, I suppose that dinosaurs would

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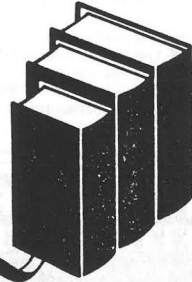
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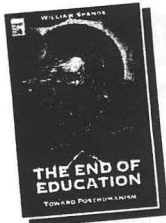
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probably still be in command (why not; they had prevailed for far longer against mammals, and mammals had been making no inroads). Mammals, if they survived at all, would probably still be small creatures no larger than rats, and small size precludes self-conscious intelligence. Dinosaurs were not moving toward higher cognition in our form, and probably could not do so. Thus you must thank the extraterrestrial impact for this copy of the *New York Review*.

But why did mammals prevail and dinosaurs die? Doesn't this fact point to some intrinsic mammalian superiority? Not necessarily. We do not know the answer, but here is one plausible scenario for a partial explanation: the rules change in mass extinction, and adaptive advantages of the past may become dangerous deficits. Large populations provide a good hedge against extinction, all other things being equal. Dinosaurs, with their massive bodies, must have maintained species of small population size. The

world must contain far fewer elephants than ants, far fewer brontosaurus than mouse-sized mammals. So perhaps mammals gained a crucial edge by large populations maintained as a consequence of small body sizes.

Now why were mammals small? Surely not because they knew that a comet would hit 10 million years down the road, and that large populations would then be useful. Presumably they were small for a negative reason in Darwin's immediate world of competition: because dinosaurs had usurped the ecological space of large terrestrial vertebrates, and relegated mammals to a periphery. Yet the reasons for relative failure in normal times may translate fortuitously to the crucial ingredient of success in prevailing through a mass extinction. The Darwinian struggle does not extrapolate to the tree of life.

Ironically, Cronin does seem to grasp this issue in her final paragraph, if only through a glass most darkly.

LETTERS

THE GUGGENHEIM STORY

To the Editors:

I enjoy and admire John Richardson's writing so much that I write with diffidence to offer a small amendment to his lively account [*NYR*, July 16] of the evolution of the Guggenheim Museum and Guggenheim antics in general. Mr. Richardson is somewhat dismissive of James Johnson Sweeney, the Director of The Guggenheim Museum from 1954 until 1960. Sweeney and I became great friends after serving together on an art jury in the fifties with Alfred Frankfurter, Editor of *Art News*, and the Director of the Chicago Art Institute. I greatly admired him. He was the first museum director in the United States concerned with modern art who presented painting and sculpture, spaciouly installed, in an all-white interior. He was quite famous for this in the fifties when we were already beginning to take the concept for granted. A man of considerable erudition and broad culture, with usually excellent judgment, Sweeney had great flair in the presentation and installation of art. He made the largest, more or less definitive retrospective exhibition of Brancusi's sculpture at the old Guggenheim Museum building at 1071 Fifth Avenue in 1955. Nobody who saw Sweeney's historic exhibition, with its tremendous spiritual charge, will ever forget it. Sweeney was also an early enthusiast for Miró and Dubuffet, acquiring many fine works by these artists for public and private collections in the United States.

Historically speaking, Sweeney was also emphatically in favor of the most radical American painting and sculpture at a time when other museum directors in the US, with the notable exception of Dorothy Miller at MOMA, were either skeptical or blew hot and cold—including the late and great Alfred Barr who tended to trace everything back to Picasso, Gonzales, or Masson. It was under the aegis of Sweeney that the superb *She Wolf* painting by Pollock was purchased for MOMA not long after it was painted in 1943, and his brother, John L. Sweeney, awarded Pollock a badly needed bursary around the same time. He was unstuffy and friendly to young artists and diligent in visiting their studios.

As Mr. Richardson records, Sweeney was sorely tried during his tenure at the Guggenheim by Harry Guggenheim's intransigence and Wright's refusal to modify his original plan. Sweeney was a museum director of real substance and his recommendations would have resulted in a build-

ing better suited from the outset to the presentation and conservation of art.

Bryan Robertson

London, England

To the Editors:

I have read the Guggenheim gospel according to John and wish to thank him for having given me equal time in the enumeration of directorial misdeeds in the history of that institution. I am not about to deny all the transgressions attributed to me, which is not to say that I plead guilty to them. But I wish to put at least some of them into context.

Since I am introduced as a "non-confrontational Czech" let me readily agree that the characterization is apt. The civilized history of my native country is marked by avoidance of hopeless conflicts and by a preference for more effective strategies. When I came to the Guggenheim as a youthful director with the almighty Harry exerting precedence over family, foundation and board, confrontational politics would have been useless and stupid. Richardson cannot possibly know what feats of courage and steadfastness were required and displayed in the privacy of our offices, nor are these recorded in the minutes for the convenience of eager research fellows. Let me merely insist here that the sale of the Kandinskys in the sixties and seventies was not "sanctioned" but initiated over some trustee opposition by myself for good and valid reasons that I am prepared to defend. As long as we are being quantitative, it might have been fair to mention that the number of Kandinsky works that left the museum during my tenure were matched by no fewer that have come to the Guggenheim through gift and purchase, virtually all through my personal intervention. I selected most of these from the collection in the Hilla Rebay Estate which, after the death of the Baroness, and after some diplomatic effort, was amicably divided between the formerly contesting parties. Both shares, the one allocated to the Guggenheim, and that which legally remains in the Rebay Estate, are now, and have been for years, in the care of the Museum and at its disposal.

The Haacke incident has been covered so extensively and the position of both parties documented so exhaustively that its current rehash in truncated form is as redundant as would be the reiteration of my retorts. Since, however, Richardson makes grateful acknowledgement to Mr. Haacke "for providing the information" I may perhaps be permitted to consider his source just a trifle one-sided.

After four hundred pages of panadaptationism, she finally recognizes that evolutionary theory must solve other problems as well—particularly the issue of shifting diversity through time—and that adaptation may not provide the basis for all answers. Darwin did wrestle brilliantly and triumphantly with the problem of adaptation, but he had limited success with the issue of diversity—even though he titled his book with reference to his relative failure: the origin of species. Cronin records and admits this irony in the last line of her book: "But, in the midst of such success, there was one problem that remained just outside his [Darwin's] grasp. It was—poignantly—the problem of the origin of species." When strict Darwinians drop their reliance on adaptation and extrapolation, and when they break bread with paleontologists in the different realm of time in millions, they will then engage this unresolved problem face to face. □

Now, as for Peggy. Richardson's statement according to which I "suggested that Peggy put the bulk of her paintings on temporary exhibit at the Guggenheim Museum, as a first step toward an eventual amalgamation of the two collections" is of course correct. Many would credit me with sagacity and perseverance for being able to make such a proposal after a more than ten years effort on behalf of my institution. But why was Peggy, as Richardson claims, "in no position to refuse" when every museum in the world courted her, willing to do almost anything to capture what then probably was the most important collection of modern art still in private hands? And why that untenable defense of John Hohnsbeen whose curatorial status was something of a joke and who did little or no work for no pay as everyone knew? When Peggy died Hohnsbeen was nowhere to be found for weeks and I couldn't have told him "to pack his things" if I had wanted to. Similarly, if after Peggy's death the family "felt no less shabbily treated" having received "not even a token item from Peggy's \$40 million, 326 piece collection" it must be stated that it was not up to the Guggenheim, indeed not permissible for that institution, to dispense gifts that were public property. Only Peggy could have done so while she owned the works, or through a provision in her will, and she did not do so. Surely, Richardson must know this.

It is true that following Peggy's death the Palazzo Venier dei Leoni with its precious collection underwent radical repair, restoration, reconstruction and facelifting inside and out. The building was literally falling into the Canal Grande and water was streaming down the adjoining Barchessa walls threatening further damage to works that had suffered neglect over the years. Ivy was eating into the facade before it was removed and the garden was a mudhole before it was paved at considerable cost to the Guggenheim. To maintain a rundown palazzo with an endangered collection as a sentimental record of Peggy's glorious life was hardly the thing to do. By accepting Peggy's gift, the Guggenheim, as a museum foundation, had assumed responsibilities which Peggy, as a private person, did not have. The decision to convert a residence into a museum was carefully arrived at, as was the earlier determination to extend the Guggenheim's collecting scope by accepting Thannhauser's early Picassos among other treasures.

But I should not be complaining, for by charging me with the incorporation of the collections in the Hilla Rebay Estate, the Justin K. Thannhauser Foundation and the Peggy Guggenheim Foundation, Richardson

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