

# Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism?

Stephen Jay Gould\*† and Elisabeth A. Lloyd‡

\*Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138; and †History and Philosophy of Science, Indiana University, 130 Goodbody Hall, Bloomington, IN 47405

Contributed by Stephen Jay Gould, June 2, 1999

Two major clarifications have greatly abetted the understanding and fruitful expansion of the theory of natural selection in recent years: the acknowledgment that interactors, not replicators, constitute the causal unit of selection; and the recognition that interactors are Darwinian individuals, and that such individuals exist with potency at several levels of organization (genes, organisms, demes, and species in particular), thus engendering a rich hierarchical theory of selection in contrast with Darwin's own emphasis on the organismic level. But a piece of the argument has been missing, and individuals at levels distinct from organisms have been denied potency (although granted existence within the undeniable logic of the theory), because they do not achieve individuality with the same devices used by organisms and therefore seem weak by comparison. We show here that different features define Darwinian individuality across scales of size and time. In particular, species-individuals may develop few emergent features as direct adaptations. The interactor approach works with emergent fitnesses, not with emergent features; and species, as a consequence of their different mechanism for achieving individuality (reproductive exclusivity among subparts, that is, among organisms), express many effects from other levels. Organisms, by contrast, suppress upwardly cascading effects, because the organismic style of individuality (by functional integration of subparts) does not permit much competition or differential reproduction of parts from within. Species do not suppress the operation of lower levels; such effects therefore become available as exaptations conferring emergent fitness—a primary source of the different strength that species achieve as effective Darwinian individuals in evolution.

## Darwinian Individuals and the Logic of Natural Selection

Manifesting the resilience of our usual metaphors for stubborn persistence—from the classical Phoenix reborn from ashes to the vernacular alley cat with nine lives—the formerly anathematized concept (1, 2) of supraorganismal selection has emerged from previous calumny to a new status of intense discussion and growing importance (3). The logic of the theory of natural selection, as many evolutionary theorists and philosophers of science have recognized (4–12), assigns the status of causal agency in selection to *interactors*, defining them as individuals that:

(i) Interact with the environment, broadly construed as all surrounding and influencing biotic and abiotic factors, in such a way that

(ii) One or more of their traits imparts differential reproductive success through the interaction, so that

(iii) Relatively more or less (compared with other individuals at their level) of their hereditary material (however packaged) passes to the next generation.

We realize, of course, that several terms in this complex definition are rich in meaning and fraught with ambiguity, and that debate continues to surround many of the issues. But the basic framework and the recognition of a proper locus of causality have now achieved general approbation.

Even though we accept this emerging consensus in favor of the interactor approach, we find that several problems still remain,

none more pressing than learning how to think about the viscerally unfamiliar (and in many ways counterintuitive) supraorganismal levels of organization and selection. (Given the reductionist traditions of Western science, we are naturally more comfortable with suborganismal units of genes and cell lineages.) We claim that evolutionists have generally not appreciated the importance of higher levels, particularly the species level of selection, because species-individuals may not build many adaptations of their own. False emphasis on adaptation therefore leads biologists to downgrade the species level as only weakly operative in the processes of selection.

We can understand how the undervaluing of species-level selection may have arisen by considering the recent literature. The sound conceptual basis for a hierarchical theory of selection has been winning respect and gaining ground during the past few years. The seminal works of D. S. Wilson and E. Sober (3, 13), based on the interactor approach, stand at the forefront of this important conceptual shift in evolutionary theory. As criteria for interactors at all levels, Sober and Wilson choose to emphasize—too restrictively, we shall argue—the properties of structural cohesion and functional design so central to our vernacular concept of conventional organisms and so vital to our practice of viewing the traits of organisms as adaptations.<sup>§</sup>

In defining their concept of an interactor, Sober and Wilson stress the “level (or levels) at which natural selection actually operates, producing the functional organization implicit in the word ‘organism’” (ref. 3, p. 591). They focus their attention on “any biological entity whose parts have evolved to function in a harmonious and coordinated fashion” (ref. 3, p. 606). But, in restricting their attention to functional integrity as a basis for adaptation, Wilson and Sober emphasize only one potential product of a process of evolution by natural selection. They claim that “higher units of the biological hierarchy can be organisms, in exactly the

†To whom reprint requests should be addressed.

<sup>§</sup>In their important 1994 article (3), though not in their 1998 book (13), Wilson and Sober proposed some ill-considered definitions. Our criticism may seem small and merely terminological, but this unfortunate choice by Wilson and Sober will, if generally adopted, impose a severe restriction upon the range of reform opened up by replacing Darwin's single-level theory of selection on organisms (or the even more reductionistic “selfish gene” proposal) with a hierarchical theory of simultaneous selection at several legitimate levels of individuality. It would be a shame to impose such a limitation at the very dawn of a theory so richly imbued with potential for radical rethinking about the basis of evolutionary causality. In their 1994 article, Wilson and Sober restricted the term “individual” to the discrete “flesh and blood” body of vernacular understanding and extended the term “organism” to designate the general concept of a Darwinian interactor as a causal unit of selection at any level of the evolutionary hierarchy. They wrote: “We use the word ‘individual’ to refer to a single flesh-and-blood creature, such as a bird or butterfly. We use the term ‘organism’ to refer to any biological entity whose parts have evolved to function in a harmonious and coordinated fashion” (ref. 3, p. 606). We, on the other hand, following ordinary vernacular usage (developed, we think, for good reasons) strongly support the opposite usage of “individual” for the general Darwinian actor at any level of the hierarchy, and “organism” for the discrete body of single creatures in Darwin's conventional realm, usually, and properly, called “organismic selection.”

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. §1734 solely to indicate this fact.

same sense that [individual bodies] are organisms, to the extent that they are vehicles of selection” (ref. 3, p. 605).

This statement suggests that if higher units operate as vehicles of selection, then they must work like organisms in the harmony and coordination of their parts. But this claim cannot be supported, for the argument confuses one potential outcome or product of a causal process with the causal process itself. Higher-level selection processes do not necessarily require, nor do they invariably produce, functional organization or harmony of parts.

In defending their definitions, Wilson and Sober claim that “no one would be interested in group selection if it never resulted in group-level adaptation” (ref. 3, p. 640). Some evolutionists do restrict their concerns in this manner; but many others do not consider group-level adaptations as a *sine qua non* for supraorganismic selection in evolution. Supporters of this broader scope of concern include Sewall Wright (14, 15), many evolutionists who maintain a Wrightian interest in population structure, and most architects of the theory of hierarchical selection (5, 16–23). More generally, the adaptationist approach establishes a mistaken and overly restrictive strategy for the analysis of species- or clade-level selection, as Williams (24) has acknowledged.

In this paper, we argue that the strategy of defining individuality by functional cohesion and adaptation of entities at all levels will stymie our understanding of the distinctive characteristics of Darwinian individuals at levels other than organismal. If we falsely restrict our concept of individuality to properties of cohesion, functionality, and adaptation, we miss the different styles of individuality—the scale-bound “allometries,”<sup>1</sup> that make evolutionary interactors at levels above and below organisms such potent and distinctive units of evolution. As happens so often in Darwinian theory, an overemphasis on adaptation promotes our failure to grasp the richness of different styles of individuality by imposing on all levels the adaptive properties of the organism—the kind of individual that we know best, if only for the intuitions inspired by our personal residence in this particular, and in many ways rather peculiar, category!

### Agency and Causality in Natural Selection

All concepts and categories in science are necessarily and inextricably theory-bound; raw nature dictates no unitary, inevitable scheme for parsing her continua. Taxonomies emerge only in the context of questions asked by investigators in their quest to understand how nature operates. Thus, the issue of what natural entities act as agents or units of selection depends crucially on the nature and logic of the theory of natural selection itself.

The central and contentious issue of causal agency in natural selection—does Darwin’s process work on organisms (as Darwin argued), on genes (as various reductionist accounts maintain), on supraorganismal units, or on some or all of these legitimate biological individuals simultaneously (as we and many others now hold)—has generated much confusion, arising not so much from dispute about empirical matters, but from conceptual problems about the nature, locus, and meaning of causality in Darwin’s

mechanism. In particular, many biologists have mistakenly equated the need for keeping a ledger of evolutionary changes through time with the task of identifying causal agents of change—a conflation of bookkeeping with causality.

David Hull’s important distinction between replicators and interactors (27) helped to clarify conceptual and empirical issues at the center of debates about units of selection. Hull modified Dawkins’ concept of a *replicator* to designate any entity that can serve as a basis for copying itself. Hull’s concept of *interactor* denotes an entity that interacts directly, as a cohesive whole, with its environment in such a way that replication becomes differential. For Hull, natural selection then becomes “a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them” (ref. 27, p. 318; cf. ref. 11, pp. 317–318).

More recently, Lloyd has analyzed the range of published positions on units of selection and evolution by distinguishing two additional entities of potential interest: the *beneficiary* and the *manifestor-of-adaptation* (refs. 28, 29; see other distinctions in refs. 11, 17, 30). Lloyd defines a beneficiary as an entity that benefits ultimately and in the long term from evolution by a selection process. A second and quite distinct version of the benefit question invokes the notion of adaptation. Evolution by a selection process may be said to benefit a particular entity under selection (at a particular level) by producing *adaptations* at that level (1, 2, 31, 32). In this approach, the entity actively selected (the interactor) *benefits* from evolution by selection at that level through its acquisition of adaptations. In this case, the entity then qualifies as a manifestor-of-adaptation. As we have emphasized above, the key insight illuminated by these distinctions leads us to recognize that not all interactors are manifestors-of-adaptations, for benefit may also accrue passively at one level when an entity at that level expresses properties as structural side consequences of causes acting at other levels. These additional criteria of manifestor and beneficiary-of-adaptations have been advanced by other authors either explicitly or by passive conflation of these intuitively appealing ideas (given the favored status of adaptation as the focal concept of Darwinian tradition) with the two categories of Hull’s classic division.

**Bookkeeping.** Replication defines the key issue in our decisions about best ways to record evolutionary results. The gene represents the most appropriate unit for marking evolutionary change for two major reasons: one has always been recognized by selfish-gene theorists but misidentified as evolutionary causality; the other, rarely acknowledged or formulated, arises from a structural property of hierarchies.

First, the gene operates as a maximally faithful replicator across generations, and bookkeepers can therefore record the evolutionary history of populations as changing relative frequencies of these stable items (as could not be done for sexual organisms, for example, because these entities disaggregate their personhood and pass only half their genotype to each offspring).

Second, genes become preferred units of bookkeeping because they represent the lowest-level individuals subject to clear and accurate recording in a genealogical hierarchy of inclusion (genes within organisms within demes within species, etc.). As a formal and general property of their structure, hierarchies of this kind manifest an important asymmetry (33), in that differential sorting at higher levels also sorts each lower level as a necessary consequence. (If, for example, some species become extinct within a clade, the relative frequencies of all lower-level individuals must change, because the extinction of a species must also remove certain kinds of organisms, certain kinds of genes, etc.). Differential sorting at lower levels, however, need not affect the frequencies of higher-level individuals at all. (The copy number of a gene may increase by gene selection within some organisms of a species without affecting the selective prowess of these organisms, or that of the deme or species containing them.) Thus, because genes are the only biological individ-

<sup>1</sup>In this paper, we obviously use the term “allometry” somewhat metaphorically. Allometry (25, 26) classically refers to differences in organismic properties (whether of form, physiology, or behavior, and whether expressed in ontogeny, phylogeny, or structural series of taxonomic relatives) that are systematically correlated (whether causally or merely descriptively and whatever the quantifiable nature of the relationship) with changes in size. In other words, allometry represents the *locus classicus* for studying the effects of scaling on organisms. But scaling in both size and time also defines the fundamental relationships of units in nature’s structural hierarchy of inclusion: genes within cell-lineages within organisms within demes within species within clades. This paper explores the question of whether the different properties that establish Darwinian individuality among the various units of nature’s hierarchy (particularly for genes, organisms, and species) arise as consequences of the fundamental scaling in size and time that pervades and defines this hierarchy. The designation of such potential differences among units as “allometric” therefore strikes us as an appropriate and potentially interesting extension of this basic biological concept.

uals reliably sorted by any process of selection acting at any level, the books of evolution are best kept at the genic level. This important conclusion about the evolutionary status of genes does not imply that genes also act as causal units or agents of natural selection.

**Defining Darwinian Individuals.** The proper definition of a Darwinian individual constitutes one of the most challenging and fascinating issues in the formulation of causality under natural selection. Three sets of criteria, ranging from conventions of ordinary language to specific requirements of Darwinian logic, define Darwinian individuality in terms of greatest generality and abstraction.

First, a biological individual must manifest the essential traits required to define such distinctive discreteness in ordinary language and not specifically as a scientific or evolutionary concept. The three properties of *distinct birthpoint*, *distinct deathpoint*, and *sufficient stability* in between will mark a biological individual as a potential Darwinian interactor by defining the difference between a discrete entity and an arbitrary segment of a smooth temporal continuum.

Second, these vernacular individuals must then manifest the two essential properties that permit them to function as evolutionary agents in genealogical systems evolving by Darwinian principles: (i) they must generate offspring (in potentially differential numbers among individuals), and (ii) these offspring must be more like them (carry more of their hereditary contributions) than like other members of the parental generation. Without such continuity in heredity, differential reproductive success will impart no Darwinian advantage to parental individuals).

Third, these evolutionary individuals must function as interactors with the environment, as defined above, so that they may be treated as Darwinian individuals, or causal agents in the process of natural selection. We might label these three sets as criteria of *vernacular*, *evolutionary*, and *Darwinian* individuality.

Individuals at several levels of an ascending structural and genealogical hierarchy manifest all these criteria nearly all the time, or at least often enough to act as important Darwinian individuals: (i) genes, if they can differentially replicate within organisms; (ii) cell lineages when not suppressed in replication by functional demands of surrounding organisms (34); (iii) organisms virtually all the time (leading to their nearly exclusive status in Darwin's own formulation); (iv) demes under conditions achieved often enough in nature (16, 17), however firmly most evolutionary biologists rejected such an idea during the 1960s and 1970s (1, 2); and (v) species nearly all the time (especially when punctuated equilibrium holds and we can reject Fisher's powerful but controvertible arguments (35) for the true existence, but necessary impotence, of selection at this level).

With this account of Darwinian individuals in hand, we can address the basic challenge: how do different-sized biological objects manifest these properties?

### The Allometry of Individuality

Biologists have long recognized the power of allometry, or alterations in form causally correlated with changes to size, to explain systematic and predictable scale dependencies in the anatomy and physiology of organisms (25, 26, 36). The differential scaling of surfaces and volumes, first codified by Galileo in 1638, defines the *locus classicus* of this subject. Haldane (ref. 37, p. 21) wrote in his most famous essay: "Comparative anatomy is largely the story of the struggle to increase surface in proportion to volume."

We might generalize the concept of allometry or scale dependency and ask whether individuality might manifest sensible changes in style across the great range of size represented by the three most widely discussed levels of an even more extensive array: the gene-individual, the organism-individual, and the species-individual. If allometric effects can be so extensive, so profound,

and so orderly within the smaller range of sizes and greater coherence of substrates represented by organisms from microscopic unicell to blue whale or sequoia tree (thus inspiring Haldane's famous remark), we might anticipate an even greater spate of interesting and systematic differences across the larger range of sizes in the hierarchy of Darwinian interactors.

In defining three principal levels of individuality—genes, organisms, and species—little debate has arisen about the last two criteria for identification: the evolutionary and Darwinian properties of individuality discussed above. That is, individuals of all three levels bear offspring more like themselves than like others in the population, and all can clearly operate as interactors in a process of selection. However, all levels of individuality do not fulfill in the same manner the three major vernacular criteria of discrete birthpoint, deathpoint, and sufficient stability.

**Bounding and Functioning.** Organisms meet these vernacular criteria with the two essential features that define our usual concept of the organic: (i) organisms are coherently bounded in space and kept recognizable in form by a physical skin that separates the self from the outside world, a distinction often buttressed by various devices—an immune system as the most prominent example—that can recognize and disarm or eliminate transgressors into the interior space; and (ii) organisms are functionally defined by interdependence and interaction among parts, such that separate units or organs (liver, heart, brain, etc.) maintain little vital meaning or potential existence in isolation and work only as adaptive components of the entirety. Needless to say, as with all definitions in the maximally various realm of natural history, even these criteria do not hold in every case; celebrated ambiguities occasionally arise, especially for colonies [the coelenterate siphonophores have served as the classic example through two centuries of debate (38, 39), for these creatures are apparently composed of genealogical organisms so specialized for different roles within the colony that they cannot exist independently and therefore function more like organs than full persons.]

But genes and species do not clearly manifest these essential features of bounding and functionality, although both levels evidently meet the defining criteria of discrete birthpoint, deathpoint, and sufficient stability. The apparent failure of species to be sufficiently "organismic" in spatially coherent packaging and functional interaction among subparts may be responsible for the common impression that, if species can be construed as Darwinian individuals at all, they cannot match conventional organisms in potential power as agents of selection. We wish to argue in this paper that entities at other levels of organization—species in particular—can operate as effectively as organisms in the role of Darwinian individual. Biologists have generally failed to appreciate this equal potential, because allometric effects at levels above and below organisms impart the requisite criteria of coherent birthpoint, deathpoint, and sufficient stability through features different from those developed by organisms.

At a level below organisms, genes achieve a form of boundedness by beginning and ending signals along the linear array of a DNA molecule, and they manifest some degree of functional organization through various devices, including repair mechanisms, for some kinds of alterations. Genes, however, do not manifest with any force even remotely approaching the capacities of organisms the functional integration that grants "sufficient stability" to organisms by regulating the sizes and interactions of subparts. Nonetheless, most genes match or exceed most organisms in stability over a full lifetime, by the different, allometrically engendered strategy of very slow cycle time for mutational change vs. intervals between replications that pass gene-offspring from one generation to the next. Thus, in the overwhelming majority of cases, genes retain sufficient stability through their lives as interactors, and therefore fulfill all vernacular criteria of individuality.



**Species Individuality.** The features that grant vernacular individuality to species depart even further, as a consequence of upward scaling in size and time, from attributes that play the same role in organisms. But “different” need not imply “worse” for setting the strength of individuality needed by Darwinian interactors to operate in processes of selection. (Here we confine our attention, as do most authors, to sexual species. The problem of defining asexual species and the debate over whether such a concept holds meaning lies outside the scope of this paper, but retains great fascination and high status as one of the most important unresolved issues in evolutionary theory.)

The species-individual manifests important properties of both boundedness and integration among subparts, but by mechanisms strikingly different from those used by organisms; the difference arises from the allometric effects of upward scaling. At the species level, the agent of bounding cannot be a physical skin, so the “shape” (or geographic range) of a species-individual presents neither a fixed form nor a predictable ontogeny; in fact, the species-individual need not even be spatially continuous, i.e., sub-sections may inhabit disjointed areas. Moreover, although species match organisms in the strength of integration among subparts, species do not achieve such integration by specialization and mutual interdependence of these subparts in the service of the whole.

Rather, species attain both properties of bounding and integration among subparts by their defining feature of reproductive isolation, which acts as the rough analog of an immune system at the organismic level. Each component of the species-individual (that is, the constituent organism-individuals) breeds successfully only with other components of the same species and also excludes similar components of different species by an inability or disinclination to mate (a defining criterion of sexual species from Buffon’s day to ours). Components of other species need not be excluded from the body space (geographic range) of the species in question. By analogy, most organism-individuals, whatever their immune defenses, tolerate myriads of commensals and parasites within their own bodies. This reproductive style of policing works effectively in maintaining the integrity of species. (Incidentally, for this primary reason, species selection can be more easily defended than inter-demic selection, where invasion from parts of other deme-individuals often threatens the integrity of the deme in question.)

### The Scaling and Limits of Adaptation in Characterizing Darwinian Individuals

Adaptation must be recognized as a potential outcome of a process of selection, not as the definition of the mechanism of selection itself. In anglophonic historical tradition<sup>||</sup> and by the logic of Darwinian functionalism,<sup>\*\*</sup> adaptation has been favored as the

<sup>||</sup>The space and nature of this forum do not permit adequate commentary on this fascinating historical issue, but Darwin’s decision to emphasize adaptation as the cardinal phenomenon facing any proper theory of life must be judged as neither idiosyncratic nor logically entailed, but rather as a sensible consequence of Darwin’s fealty to a distinctively English tradition in natural history dating back to foundational works by Boyle and Ray in the late 17th century, and culminating in Paley’s *Natural Theology* of 1802. The Argument From Design—the claim that God’s existence and attributes lie revealed in the exquisite design of organisms and the harmony of ecosystems—formed the centerpiece of this particular tradition, in clear distinction from most continental preferences for locating God’s hand in the taxonomic order (the “laws of form”) pervading the interrelationships of organisms. British natural theologians used the vernacular word “adaptation” to describe this exquisite design that presumably flowed from God’s creative grace. The essence of Darwin’s philosophical radicalism lies in his decision to retain the core problem (the explanation of good design, or adaptation) while utterly inverting the Paleyan explanation by substituting organisms struggling for their individual advantage for God’s overarching and benevolent intent.

<sup>\*\*</sup>Most famously expressed by Darwin himself in a familiar passage from the *Introduction* to the *Origin of Species* (ref. 40, p. 3): “It is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been

preeminent subject of evolutionary analysis; this focus has recently (43) and in the past (41, 42) been vigorously challenged for different reasons. Given the persistence of this loyal opposition and the important theoretical separation of mechanism and effect (in this case, the status of adaptation as one class of effects, however traditionally favored among potential alternatives), we must question the common use of achieved adaptation as a primary criterion for the strength of a selective process.

The interactor criterion for defining natural selection as a causal process requires that a trait of a Darwinian individual impart a level-specific component of fitness to that individual through a correlation of the trait with the selective internal and external environment. Nothing in the logic of this definition requires that the trait providing such fitness be an adaptation of the Darwinian individual at the level of its immediate interaction. The trait need only impart a unique component of fitness; it does not have to rank as an emergent character of the Darwinian individual under consideration.<sup>††</sup>

Species selection becomes especially interesting in evolutionary theory as a locus of interacting effects from several levels of organization, whereas the traditional organismic level works more by suppression and exclusivity, that is, by using its considerable power to build adaptations at its own level and by excluding effects from other levels. Almost by definition (of behavior in random systems), such effects must be deleterious to the precisely maintained functional integrity of the organism; for any trait built at another level must be viewed as effectively random with respect to its operation at a new focal level.

For example, in the case that inspired our previous paper (45), and that may rank as most important in evolution by virtue of generality, the *variability* of traits within species often imparts an emergent component of fitness to the species as a Darwinian individual. But variability represents an ensemble or aggregate trait; variability therefore cannot be regarded as an emergent character of the species. (Emergent traits at any level must arise by interaction among constituent parts—in the case of species-individuals, among organisms.) As an aggregate character, variability need not be construed as an adaptation at the species level.

The common, and often unconscious, bias of defining the salience of an evolutionary process by its role in the production, maintenance, or utilization of adaptations has stymied our understanding of selection at supraorganismic levels, where adaptation may not hold the definitive status generally granted to this result in the organismic realm. This error has been catholic in distribution; for both supporters and denigrators of supraorganismic selection and of the interactor approach have mistakenly linked the defense of their contrary positions to the presence and production of adaptations.

Hull, for example, coined the term “interactor” for the active causal agent in evolution by selection, but he nevertheless held that the validation of supraorganismic selection depends on “whether entities more inclusive than organisms exhibit adaptations” (ref. 27, p. 325). Several of the strongest supporters of species selection, including an author of this paper in previous work (33), have linked their defense to the identification of emergent characters arising as adaptations at the species level; whereas they should have used the broader, more justifiable, and more fully operational emergent fitness approach.

modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration.”

<sup>††</sup>The emergent fitness vs. emergent character criterion has sparked an interesting debate (5, 21). One of us (S.J.G.) formerly preferred the latter alternative (33) before being persuaded by the other (E.A.L.) of the greater validity of the fitness criterion for theoretical reasons rooted in the logic of selection as a causal process and for practical reasons (the imperfection of historical records—see below). Grantham (44) provides a good account of this debate and of our suggested resolution.

Detractors of both supraorganismal selection and the interactor approach have often, in a strange irony, grasped and explicated the concept of interaction with skill and understanding, but have then rejected the interactor approach to defining evolutionary causality because they correctly recognized its disconnection with the concept of adaptation. But they erred in using adaptation as the necessary and sufficient criterion for inferring evolutionary causality. Williams (24), for example, provides the finest description of the interactor approach ever written, but then wrongly locates causality in an alternate “codical” realm of replicating information rather than in the material domain of Darwinian individuals (see analysis in ref. 35). As one author (E.A.L.) of the present paper argued (29), Dawkins (46) also rejects the interactor (“vehicle” in his terminology) approach, and, although he explicates the concept with force and accuracy, he confuses questions about “beneficiaries” and “manifestors-of-adaptations” with the identification of interactors as causal agents in selection. Lloyd (29) writes of Dawkins: “He begins by admitting that groups can function as interactors. His argument that groups should not be considered real units of selection amounts to the claim that the groups are not the ultimate beneficiaries.” In misidentifying replicators as primary causal units, Dawkins appeals to their role as beneficiaries of adaptations and denies interactors their appropriate causal status: “It is still genes that are regarded as replicators which actually survive (or fail to survive) as a consequence of the (vehicle) selection process” (ref. 46, p. 100). Dawkins’ inability to grasp the causal role of interactors in selection processes arises from his limited focus on a particular problem that motivates his personal interest: namely, what is “the nature of the entity *for whose benefit* adaptations may be said to exist” (ref. 46, p. 81; our emphasis). Unfortunately, Dawkins interprets all claims for supraorganismal selection as requiring statements about beneficiaries and manifestors of adaptations as well as about interactors; and this overextended definition leads to a serious misreading of authors who pursue the interactor question alone, as we do here.

**Adaptations: Organisms vs. Species.** By virtue of their defining properties of boundedness in form and interactivity of parts, organisms—the Darwinian individuals that we must know best for the most ineluctably personal of reasons—become functional units replete with adaptations as a consequence of Darwinian processes. But suppose—as we believe to be the case—that this proneness to develop adaptations represents an allometrically based property of organismic individuality that does not translate with similar intensity to the construction of individuality at other levels, where disparate ranges of size and time enjoin different properties to meet the defining criteria. In particular, species-individuals may develop relatively few species-level adaptations, not as a mark of weakness for species as Darwinian interactors, but as an allometric property of individuality at this level. Perhaps the most interesting difference between the organism and the species as evolutionary and Darwinian interactors lies in the difficulty of building adaptations when reproductive exclusivity among subparts (rather than boundedness of overall form and functional interaction among constituent parts) defines individuality, thereby allowing species-individuals to interact with the environment through traits that are not species-level adaptations. The emergent fitness approach works especially well in identifying traits that may not exist as adaptive characters of the species, but may impart fitness by upward causation from lower levels (5). Such traits, originating for causal reasons at other levels, achieve expression as “side consequences” at the species level, where they may then become important, even vital, exaptations (47)<sup>‡‡</sup> by imparting useful effects (emergent fitness in this case) to the species-individual.

<sup>‡‡</sup>Gould and Vrba (47) defined exaptations as features evolved for one reason (whether or not as adaptations), and then coopted for utility in another role; the bird feather, evolved for thermoregulation and later coopted for flight, for example. Such coopted structures cannot

We do not, of course, hold that species develop no genuine species-level adaptations as truly emergent traits. But we do emphasize two features that make the identification of emergent traits a poor primary criterion for identifying species selection:

(i) Emergent characters are difficult to define because their elucidation usually requires considerable historical knowledge of details in the ancestral history of particular lineages to distinguish truly emergent traits from cascading effects of properties built at other levels. Such density of historical information can rarely be obtained from imperfect fossil records.

(ii) Emergent characters represent only a (perhaps low-frequency) subset of traits that can serve species-individuals by imparting emergent species-level fitness in a causal process of interaction with the environment.

The paucity of well-documented cases has been proposed with apparent force, after many years of discussion, as a telling argument against the general efficacy or even the existence of species selection. But current failure may represent an artifact of using the overly restrictive and often nonoperational criterion of emergent characters, inspired by misplaced emphasis on adaptation. Only emergent traits can rank as adaptations at the species level; we will unnecessarily restrict our explanatory compass if we use the generation of adaptations, rather than the proper criterion of fitness in interaction, to define causal agency in natural selection. If we move to the far less restrictive and theoretically preferable criterion of emergent fitness—a fully operational proposition requiring no historical knowledge of the level of origin or adaptive status of a trait—then we may reconceive species selection as not only fully testable, but also potent and potentially ubiquitous.

## Conclusions

The most salutary effect of this rethinking lies in its potential for breaking a conceptual logjam that has effectively precluded fruitful research on this subject. Once we understand that to function well as Darwinian interactors, species-individuals either may or may not develop design-type adaptations, then we may clearly distinguish two vital questions for research. The previous conflation of these questions has long stymied progress in this important domain of evolutionary theory.

(i) Do species function as Darwinian individuals and interactors with an active and significant role in evolution by selection?

(ii) Does the evolution of species-level interactors produce species-level engineering adaptations, and if so, how often?

For most of the history of the species selection debate, these two questions have been treated as identical. In other words, asking whether species could be construed as units of selection meant asking whether species operated both as interactors and as manifestor-of-adaptations.

The desired breakthrough may result from the proper separation of these two questions, and from the different answers given to each: a resounding “yes” to the first, and a “not very often, given the allometric properties that define individuality at the species level” to the second. With this principled separation, we may finally identify the distinctive and primary power of the species-individual as a Darwinian interactor, a strength that arises from scale-bound allometric features and precludes an important role for direct

properly be called adaptations for current usage, because they did not evolve to work in their present manner. Yet such structures may be as useful to the organism, as essential to survival and as biomechanically fit (however fortuitously so) to a new usage as any feature explicitly evolved for its current function. Thus, Gould and Vrba suggested that this previously unnamed category of structures with coopted utility be called “exaptations,” that is, taken from a former (*ex*) state, for utility (*apt*) in a new role, rather than adaptations, designed for (*ad*) their current utility (*apt*). The concept of exaptation implies an obvious and principled extension to the passage of effects across levels of organization: If a feature evolved at one level produces automatic and consequential effects on Darwinian individuals at a higher or lower level, these effects, if then used at the new level, must be called exaptations. Their source and origin lie at another level, and their original function, if any, must be different from their current function in the focal individual now benefiting from the emergent fitness they provide.

adaptation by emergent traits at the species level. The organism, in securing individuality by boundedness and functional integration of subparts, has evolved powerful mechanisms to suppress selection at lower levels within itself, lest internal proliferation of some subparts at the expense of others discombobulate the functional operation of the whole and eventually kill the organism. As Buss (34) shows in his important book, organisms thus effectively cut off selective proliferation at the next lower level of the cell-lineage. (When they fail to do so, we call the outcome cancer.) At the still lower gene level, selection within organisms can be more effective, because up to a certain point, proliferation of multiple copies of genes within the genome may not affect the organismal phenotype, thereby escaping “notice” by the evolved policing systems of organismic integrity.

The sexual species does not so rigidly suppress the selection of subparts within itself, having neither the need nor the opportunity to do so. The sexual species, maintaining individuality primarily by the reproductive exclusivity of subparts (organisms), cannot be strongly threatened by differential proliferation of these subparts. Some features of populations, gene flow for example, could be interpreted as mechanisms of suppression by spreading and dilution, but such features can also transform the species-individual from within. All mechanisms of transformation from within, including ordinary anagenetic change by conventional organismic selection, act as higher-level analogs of Lamarckism, and provide a distinctive source of evolutionary potency for species-individuals, rendered all the more curious and interesting as an allometric effect because the organismic level, as a defining feature, actively precludes any comparable mechanism for adaptive transformation from within during a single lifetime. In any case, the species maintains no evolutionary interest in such general and effective suppression, for differential proliferation of subparts often works to the selective advantage of species, either by adaptive anagenetic transformation or by production of new and different daughter species. The analogous situation at the lower level usually spells disaster for organisms, thus establishing one of the most interesting and important allometric differences between levels of evolutionary organization.

The species-individual, by not suppressing selection at lower levels within itself, thereby maintains a large reservoir of nonemergent, sum-of-the-parts traits that are built at these lower levels but provide potential exaptive benefit to the species. These traits cannot be viewed as actively evolved adaptations at the species level; but they can (and probably do) provide a major component of emergent

fitness, crucial to the success of species-individuals in the process of species selection. One might argue that such nonsuppression of lower levels defines and establishes the most distinctive power of the species as a Darwinian individual. For the species-individual then meets the external world with an extensive suite of both actual and latent fitness providers, built at several levels, but all working to its advantage—including some genuine species-level adaptations assembled from emergent traits and a larger set of potential cross-level exaptations provided by upward causation from traits actively evolving at lower levels and thereby able to impart emergent fitness to the species-individual.

We therefore venture the following ironic conclusion about distinctive allometric features of the species as a source of strength in selection.

The species-individual, as a Darwinian interactor in selection at its own level, operates largely with cross-level exaptations arising from unsuppressed evolution of subparts (primarily organisms) at lower levels within itself. Such nonsuppression acts as a source of power by permitting species to draw upon a wider pool of features than organisms can access (for the organismic style of individuality enjoins active suppression of most selection at lower levels within itself).

By *not* suppressing this evolutionary churning from within, the species-individual gains enormous flexibility in remaining open to help from below, expressed as exaptive effects that confer emergent fitness. Rather than viewing this nonsuppression of aid from other levels, with the accompanying failure to build many active adaptations at its own level, as a sign of wimpy weakness for the species—construed as a “poor organism” in the implication of most traditional thought—we should rather interpret these allometrically driven properties as cardinal strengths, and recognize the species as a “rich-but-different” Darwinian individual. The species, in this view, acts as a shelter or arbor that holds itself fast by active utilization of the properties that build its well-defined individuality. By not suppressing internal change and thereby gaining a large supply of upward cascading exaptive effects, species use the features of all contained lower-level individuals through the manifestation of their effects on the shelter itself. The species, through its own distinctive features of individuality, and requiring neither indulgence nor apologia from human understanding, will continue to operate as a powerful agent in Darwin’s world whether or not we parochial organisms, limited by our visceral feelings and traditions of language, choose to expand our view and recognize the sources of evolutionary potency at distant scales of nature’s hierarchy.

- Williams, G. C. (1966) *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, NJ).
- Maynard Smith, J. (1976) *Q. Rev. Biol.* **51**, 277–283.
- Wilson, D. S. & Sober, E. (1994) *Behav. Brain Sci.* **17**, 585–654.
- Griesemer, J. R. & Wade, M. (1988) *Biol. Philos.* **3**, 67–96.
- Damuth, J. & Heisler, I. L. (1988) *Biol. Philos.* **3**, 407–430.
- Lloyd, E. A. (1988) *The Structure and Confirmation of Evolutionary Theory* (Greenwood, Westport, CT).
- Sober, E. (1984) *The Nature of Selection: Evolutionary Theory in Philosophical Focus* (MIT Press, Cambridge, MA).
- Sober, E. & Lewontin, R. C. (1982) *Philos. Sci.* **47**, 157–180.
- Wimsatt, W. (1980) in *Scientific Discovery: Case Studies*, ed. Nickles, T. (Reidel, Dordrecht, the Netherlands).
- Wimsatt, W. (1981) *Proc. Philos. Sci. Assoc.* **1**, 122–183.
- Brandon, R. N. (1982) *Proc. Philos. Sci. Assoc.* **2**, 315–323.
- Brandon, R. N. (1990) *Adaptation and Environment* (Princeton Univ. Press, Princeton, NJ).
- Sober, E. & Wilson, D. S. (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard Univ. Press, Cambridge, MA).
- Wright, S. (1931) *Genetics* **16**, 97–159.
- Wright, S. (1980) *Evolution* **34**, 825–843.
- Wade, M. J. (1978) *Q. Rev. Biol.* **53**, 101–114.
- Wade, M. J. (1985) *Am. Nat.* **125**, 61–73.
- Goodnight, C. J. (1990) *Evolution* **44**, 1614–1624.
- Goodnight, C. J. (1990) *Evolution* **44**, 1625–1636.
- Goodnight, C. J., Schwartz, N. M. & Stevens, L. (1992) *Am. Nat.* **140**, 743–761.
- Arnold, A. J. & Fristrup, K. (1982) *Paleobiology* **8**, 113–129.
- Uyenoyama, M. K. & Feldman, M. W. (1980) *Theor. Popul. Biol.* **15**, 58–85.
- Uyenoyama, M. K. & Feldman, M. W. (1980) *Theor. Popul. Biol.* **17**, 340–414.
- Williams, G. C. (1992) *Natural Selection: Domains, Levels and Challenges* (Princeton Univ. Press, Princeton, NJ).
- Huxley, J. S. (1932) *Problems of Relative Growth* (MacVeigh, London).
- Gould, S. J. (1966) *Biol. Rev.* **41**, 587–640.
- Hull, D. L. (1980) *Ann. Rev. Ecol. Syst.* **11**, 311–332.
- Lloyd, E. A. (1992) in *Keywords in Evolutionary Biology*, eds Keller, E. F. & Lloyd, E. A. (Harvard Univ. Press, Cambridge, MA).
- Lloyd, E. A. (1999) in *Thinking About Evolution: Historical, Philosophical and Political Perspectives*, eds Singh, R., Krimbas, C., Paul, D. & Beatty, J. (Cambridge Univ. Press, New York).
- Mitchell, S. D. (1987) *Philos. Sci.* **54**, 351–367.
- Eldredge, N. (1985) *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought* (Oxford Univ. Press, New York).
- Vrba, E. (1984) *Syst. Zool.* **33**, 318–328.
- Vrba, E. & Gould, S. J. (1986) *Paleobiology* **12**, 217–228.
- Buss, L. (1987) *The Evolution of Individuality* (Princeton Univ. Press, Princeton, NJ).
- Gould, S. J. (1994) *Proc. Natl. Acad. Sci. USA* **91**, 6764–6771.
- D’Arcy Thompson, W. (1917) *On Growth and Form* (Macmillan, London).
- Haldane, J. B. S. (1927) *Possible Worlds* (Chatto & Windus, London).
- Huxley, T. H. (1858) *The Oceanic Hydrozoa* (The Ray Society, London).
- Haeckel, E. (1888) *Report on the Siphonophorae* (Zoology of the Challenger Expedition, Part 77, London).
- Darwin, C. (1859) *The Origin of Species* (Murray, London).
- Galton, F. (1889) *Natural Inheritance* (Macmillan, London).
- Bateson, W. (1894) *Materials for the Study of Variation* (Macmillan, London).
- Gould, S. J. & Lewontin, R. C. (1979) *Proc. R. Soc. Lond. B* **205**, 581–598.
- Grantham, T. A. (1995) *Annu. Rev. Ecol. Syst.* **26**, 301–321.
- Lloyd, E. A. & Gould, S. J. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 595–599.
- Dawkins, R. (1982) *The Extended Phenotype: The Gene as the Unit of Selection* (Oxford Univ. Press, Oxford).
- Gould, S. J. & Vrba, E. S. (1982) *Paleobiology* **8**, 4–15.