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Gulliver's further travels: the necessity and difficulty of a hierarchical theory of selection

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For principled and substantially philosophical reasons, based largely on his reform of natural history by inverting the Paleyan notion of overarching and purposeful beneficence in the construction of organisms, Darwin built his theory of selection at the single causal level of individual bodies engaged in unconscious (and metaphorical) struggle for their own reproductive success. But the central logic of the theory allows selection to work effectively on entities at several levels of a genealogical hierarchy, provided that they embody a set of requisite features for defining evolutionary individuality. Genes, cell lineages, demes, species, and clades—as well as Darwin's favoured organisms—embody these requisite features in enough cases to form important levels of selection in the history of life.

R. A. Fisher explicitly recognized the unassailable logic of species selection, but denied that this real process could be important in evolution because, compared with the production of new organisms within a species, the origin of new species is so rare, and the number of species within most clades so low. I review this and other classical arguments against higher-level selection, and conclude (in the first part of this paper) that they are invalid in practice for interdemic selection, and false in principle for species selection. Punctuated equilibrium defines the individuality of species and refutes Fisher's classical argument based on cycle time.

In the second part of the paper, I argue that we have failed to appreciate the range and power of selection at levels above and below the organismic because we falsely extrapolate the defining properties of organisms to these other levels (which are characterized by quite different distinctive features), and then regard the other levels as impotent because their effective individuals differ so much from organisms. We would better appreciate the power and generality of hierarchical models of selection if we grasped two key principles: first, that levels can interact in all modes (positively, negatively, and orthogonally), and not only in the negative style (with a higher level suppressing an opposing force of selection from the lower level) that, for heuristic and operational reasons, has received almost exclusive attention in the existing literature; and second, that each hierarchical level differs from all others in substantial and interesting ways, both in the style and frequency of patterns in change and causal modes.

Keywords: Fisher, R. A.; species; scaling and allometry; species selection; hierarchical selection; punctuated equilibrium

1. THE VALIDITY AND NECESSITY OF SELECTION AT SUPRAORGANISMIC LEVELS, WITH EMPHASIS ON SPECIES SELECTION

(a) *R. A. Fisher and the compelling logic of species selection*

R. A. Fisher added a short section entitled 'the benefit of species' to the second edition (1958) of his founding document for the Modern Synthesis *The genetical theory of natural selection* (first published in 1930). I do not know why he did so, but I (as a proponent of species selection) could not be more pleased by the content—for Fisher, in these few additional paragraphs, supplies the two features most needed by any healthy and controversial theory. Fisher proclaims the logic of species selection unassailable, and then denies that this genuine phenomenon could have any substantial importance in the empirical record of evolution on our planet. No promotor of species selection could possibly ask for more from a great thinker like Fisher than validation in logic and a healthy dispute about actual evidence!

Fisher begins this interpolated passage by stating that 'Natural Selection' (his upper-case letters), in the conventional organismic mode, cannot explicitly build any features for 'the benefit of the species' (though organismic adaptation may engender such an effect as a side consequence). Speaking of instinctual behaviours, Fisher writes (1958, p. 50): 'Natural Selection can only explain these instincts in so far as they are individually beneficial, and leaves entirely open the question as to whether in the aggregate they are a benefit or an injury to the species.' But Fisher then recognizes that, in principle, selection among species could occur, and could lead to higher-level adaptations directly beneficial to species. However, lest this logical imperative derail his strict Darwinian commitments to the primacy of organismic selection, Fisher then adds that species selection—though clearly valid in logic and therefore subject to realization in nature—must be far too weak (relative to organismic selection) to have any practical effect upon evolution. I regard the following lines (Fisher 1958, p. 50) as one of the 'great quotations' in the history of evolutionary thought:

'There would, however, be some warrant on historical grounds for saying that the term Natural Selection should include not only the selective survival of individuals of the same species, but of mutually competing species of the same genus or family. The relative unimportance of this as an evolutionary factor would seem to follow decisively from the small number of closely related species which in fact do come into competition, as compared to the number of individuals in the same species; and from the vastly greater duration of the species compared to the individual.'

Fisher's theoretical validation of the logic behind species selection has never been challenged. Even the most ardent gene selectionists have granted this point, and have dismissed species selection from extensive consideration only for its presumed weakness relative to their favoured genic level, and not because they doubt the validity, or even the reality, of selection at this higher level. Dawkins (1982, pp. 106–107) has sharpened Fisher's point by noting that, at most, species selection might accentuate some relatively 'uninteresting' linear trends (like size increase among species in a lineage), but could not possibly 'put together complex (organismal) adaptations such as eyes and brains'. Dawkins continues:

'When we consider the species as a replicator . . . the replacement cycle time is the interval from speciation event to speciation event, and may be measured in thousands of years, tens of thousands, hundreds of thousands. In any given period of geological time, the number of selective species extinctions that can have taken place is many orders of magnitude less than the number of selective allele replacements that can have taken place. . . . We shall have to make a quantitative judgment taking into account the vastly greater cycle time between replicator deaths in the species selection case than in the gene selection case.'

I strongly support Dawkins's last statement, and will argue that, when we factor punctuated equilibria into the equation, species selection emerges as a powerful force in macroevolution (though not as an architect of complex organismic adaptations).

Williams has also supported Fisher's argument about the logic of higher level selection even in his gene selectionist manifesto of 1966, where he defends the possibility, but then denies the actuality: 'If a group of adequately stable populations is available, group selection can theoretically produce biotic adaptations, for the same reason that genic selection can produce organic adaptations' (Williams 1966, p. 110). In his later book, however, Williams becomes much more positive about the importance and reality of selection at several hierarchical levels: 'To Darwin and most of his immediate and later followers, the physical entities of interest for the theory of natural selection were discrete individual organisms. This restricted range of attention has never been logically defensible' (Williams 1992, p. 38).

The developing literature has added three 'classical' arguments against higher-level selection to Fisher's primary point that cycle times are incomparably slow relative to the lives of organisms. All these arguments share the favourable property of accepting a common logic but challenging the empirical importance of legitimate phenomena—a far happier state for productive science than the confusion about concepts and definitions that so often reigns. In the rest of this section, I shall summarize

the four classical arguments; note that they can all be effectively challenged at the level—'group,' or interdemic, selection—for which they were devised; and then demonstrate that none have any strong force, in principle, against the empirical importance of the still higher level of species selection.

(b) *The classical arguments against efficacy of higher-level selection*

The usual arguments against higher-level selection, all quite potent, admit that such phenomena must be possible in principle, but cannot play any meaningful role in evolution on grounds of rarity and weakness relative to ordinary natural selection upon organisms.

1. Weakness (based on cycle time); R. A. Fisher's classical argument. How could species selection have any substantial effect upon evolution? Rate and effect depend upon numbers and timings of births and deaths—to provide a sufficient population of items for differential sorting. But species persist for thousands or millions of years, and clades count their 'populations' of component species in tens, or at most hundreds, and not as the millions or billions of organisms in many populations. How could species selection have any measurable effect at all (relative to ordinary organismic selection) when, on average, billions of organismic births and deaths occur for each species origin or extinction, and when populations of organisms contain orders of magnitude more members than populations of related species in a clade?
2. Weakness (based on variability). Hamilton (1971), in devising arguments against interdemic selection, pointed out that variation among mean group values for genetically relevant and selected aspects of organismic phenotypes will generally be lower than variation among organisms within a population for the same features. Group selection cannot be strong if the mean phenotypes of demic individuals express such limited variation to serve as the raw material of change.
3. Instability, as in Dawkins's (1982) metaphors of dust-storms in the desert and clouds in the sky. This argument has also been urged most strongly against interdemic selection. Demes, by definition, have porous borders because organisms in the same species can interbreed, and members of one deme can therefore, in principle, invade and join another in a reproductive role. If such invasions are frequent and numerous, the deme ceases to be a discrete entity, and cannot be called an evolutionary individual (thereby losing any status as a potential unit of selection). Furthermore, many demes lack cohesion on their own account, and not only by susceptibility to incursion. Demes may be entirely temporary and adventitious aggregates of organisms, devoid of any inherent mechanism for cohesion, and defined only by the transient and clumpy nature of appropriate habitats that may not even persist for a requisite generation—the deme of all mice in a haystack, or all cockroaches in a dirty urban kitchen, for example.
4. Invasibility from other more potent levels, usually from below. This standard argument, related to Fisher's first point about cycle time, and classically used to question

the potential evolution of altruism by interdemic selection, asks how higher-level selection could possibly be effective when more powerful, lower-level invaders can cancel any result by working in the opposite direction. More particularly, suppose that interdemic selection is cranking along at its characteristic pace, increasing the overall frequency of altruistic alleles in the entire species because demes with altruists enjoy differential success in competition against demes without altruists. This is fine, but as soon as a selfish mutant arises in any deme with altruists, its advantage in organismic selection against the altruistic allele should be so great that the frequency of altruistic genes must plummet within the deme, even while the deme profits in group selection from the presence of altruistic organisms. By Fisher's argument of cycle time, organismic selection of the self-serving should trump interdemic selection for altruism.

(c) ***Overcoming these classical arguments, in practice for interdemic selection, but in principle for species selection***

As most modern debate about higher-level selection has addressed interdemic (or so-called 'group') selection, the classical arguments have been framed mainly at the level just above our conventional focus upon organisms (though I predict that emphasis will shift to higher levels, particularly to species selection, as macroevolutionary theory develops). All four arguments have force, and do spell impotency (or even incoherence and nonexistence) for interdemic selection in many circumstances. But, as generalities, these arguments have failed either to disprove interdemic selection as a meaningful force worthy of consideration at all, or to deny the efficacy of interdemic selection in certain important circumstances.

I shall not review this enormous literature (as my primary concern rests at still higher levels of selection), but I wish to note that two classes of argument grant interdemic selection sufficient strength and presence to count as a potentially great force in evolution. First, much mathematical modelling (and some experimental work) has adequately shown that, under reasonable conditions of potentially frequent occurrence in nature, group selection can assert its sway against the legitimate force of the four classical objections. In the cardinal example, under several plausible models, the frequency of altruistic alleles can increase within a species, so long as the rate of differential survival and propagation of demes with altruistic members (by group selection) overcomes the admitted decline in frequency of altruists within successful demes by organismic selection. The overall frequency may rise even while the frequency within each surviving deme declines (Wilson 1983).

Second, some well documented patterns in nature seem hard to explain without a strong component of interdemic selection. Female-biased sex ratios, as discussed by Wilson & Sober (1994, pp. 640–641), provide the classic example because two adjacent levels make opposite and easily tested predictions: conventional organismic selection should favour a 1:1 ratio by Fisher's famous argument (1930); whereas interdemic selection should promote strongly female-biased ratios to enhance the productivity of groups. Williams (1966) accepted this framework,

which he proposed as a kind of acid test for the existence of group selection. He allowed that female-biased ratios would point to group selection, but denied that any, in fact, existed, thus validating empirically the theoretical arguments he had developed for the impotency of group selection. Williams concluded (1966, p. 151): 'Close conformity with the theory is certainly the rule, and there is no convincing evidence that sex ratios ever behave as a biotic adaptation.' But many empirical examples of female-biased ratios were soon discovered (see Colwell (1981), and numerous references in Wilson & Sober (1994, p. 592)). Some authors (Maynard Smith 1987, for example) tried to interpret this evidence without invoking group selection, but I think that all main participants in the discussion now admit a strong component of interdemic selection in such results—and reported cases now number in the hundreds, so we are not talking about odd anomalies in tiny corners of nature. Williams now accepts this interpretation (1992, p. 49), writing 'that selection in female-biased Mendelian populations favors males, and that it is only the selection among such groups that can favor the female bias'.

The primary appeal of this admirably documented example lies in the discovery that female biases are usually only moderate—more than organismic selection could allow (obviously, as any bias at all would establish the point), but less than models of purely interdemic selection predict. Thus, the empirical evidence suggests a balance between adjacent and opposing levels of selection—with alleles for female-biased sex ratios reduced in frequency by organismic selection within demes, but boosted above the Fisherian balance (across species as a whole) because they increase the productivity of demes containing them at high frequency.

When we move to the level of species selection, the most important for macroevolutionary theory, we encounter an even more favourable situation. For interdemic selection, the classical contrary arguments had legitimate force, but could be overcome under conditions broad enough to grant the phenomenon considerable importance. For species selection, on the other hand, most of the classical arguments don't even apply in principle—while the one that does (weakness caused by cycle time) becomes irrelevant if punctuated equilibrium prevails at a dominant relative frequency.

Proceeding through the classical objections in reverse order, the fourth argument about invasibility from below has strength only in particular contexts—when, in principle, a favoured direction of higher-level selection will usually be opposed by stronger selection at the level immediately below. (In the classic case, selfish organismal 'cheaters' derail group selection for altruism. Nonetheless, while the argument of invasibility may hold for this particular case—and while, for contingent reasons in the history of science, this example became the paradigm for interdemic selection—I see no reason, in principle, for thinking that organismal selection must always, or even usually, oppose interdemic selection. The two levels may operate simultaneously and in the same direction, or orthogonally.)

In any case, I cannot devise any rationale for supposing that organismic or interdemic selection should characteristically oppose species selection—and the argument of

invasibility therefore collapses. Of course, organismic selection may operate contrary to the direction of species selection—and must frequently do so, particularly in the phenomenon that older textbooks called ‘overspecialization,’ or the development of narrowly focused and complex adaptations (the peacock’s tail as a classic example) that enhance the reproductive success of individual organisms, but virtually guarantee a decreased geological life span for the species. But other equally common modes of organismic selection either tend to increase geological longevity (improvements in general biomechanical design, for example), or to operate orthogonally, and therefore ‘beneath the notice’ of species selection. As our best examples of species selection work through differential rates of speciation rather than varying propensities for extinction, and as most organismal adaptations probably don’t strongly influence a population’s rate of speciation (or at least don’t manifest any bias for decreasing the rate), essential orthogonality of the two levels must often prevail in evolution.

The third argument of instability, while potent for demes, clearly does not apply to species, which are as well bounded as organisms. Just as genes and cell lineages generally do not wander from organism to organism (while organisms often move readily from deme to deme), neither can organisms or demes wander from species to species. The reasons for such tightness of bounding differ between organism and species, but these two evolutionary individuals probably exceed all others in strength of this key criterion. Species maintain and ‘police’ their borders just as well as organisms do.

The tight bounding of an organism arises from functional integration among constituent parts, including an impermeable outer covering in most cases, and often an internal immune system to keep out invaders. The tight bounding of a species arises from reproductive interaction among parts (organisms), with firm exclusion of parts from any other species. Furthermore, this exclusion is actively maintained, not merely passively propagated, by properties that became a favourite subject of study among founders of the Modern Synthesis, especially Dobzhansky (1951) and Mayr (1963)—the so-called ‘isolating mechanisms’. Species may lack a literal skin, but they are just as well-bounded as organisms in the sense required by the theory of natural selection.

This discussion highlights one of my few reservations with Wilson & Sober’s (1994) excellent discussion and defence of hierarchical selection. They insist upon functional integration as the main criterion for identifying units of selection (vehicles in their terminology, interactors or evolutionary individuals for others). They insist that the following question ‘is and always was at the heart of the group selection controversy—can groups be like individuals in the harmony and coordination of their parts?’ (1994, p. 591).

I do not object to the invocation of functionality itself, but rather to their narrow definition, too parochially based upon the kind of functionality that organisms display. The cohesion (or ‘functionality’) of species does not lie in the style of interaction and homeostasis that unites organisms by the integration of their tissues and organs. Rather, the cohesion of species rests upon their active maintenance of distinctive properties, achieved by

interdigitating their parts (organisms) through sexual reproduction, while excluding the parts of other species by evolution of isolating mechanisms.

I much prefer and support Wilson & Sober’s more general definition (1994, p. 599): ‘Groups are real to the extent that they become functionally organized by natural selection at the group level.’ Species meet this criterion by evolving species-level properties that maintain their cohesion as evolutionary individuals. The key to a broader concept of ‘functionality’ (that is, the ability to operate discretely as a unit of selection) lies in the evolution of active devices for cohesion, not in any particular style of accomplishment—either the reproductive barriers that maintain species, or the homeostatic mechanisms that maintain organisms.

The second argument of weakness based on lack of sufficient variability among group mean values also does not apply to species. Demes of mice from separate adjacent haystacks may differ so little in group properties that the survival of only one deme, with replenishment of all haystacks by migrants from this successful group, might scarcely alter either allelic frequencies across the entire species, or even average differences among demes. But new species must differ, by definition, from all others—at least to an extent that prevents reproductive merging of members. Thus, the differential success of some species in a clade must alter—usually substantially—the average properties of the clade (while, one level down, the differential success of some demes need not change the average properties of the species very much, if at all).

We are thus left with the first argument about weakness caused by long cycle time and small populations, as the only classical objection with potential force against species selection. At first glance, Fisher’s argument would seem both potent and decisive. The basic observation is surely true: billions of organism births usually occur for each species birth; and populations of organisms within a species are almost always vastly larger than populations of species in a clade. How then could species selection, despite its impeccable logic, have any measurable importance when conventional organismal selection must be so incomparably stronger?

The logic of Fisher’s argument is undeniable, but we must also consult the empirical world. Organismic selection must overwhelm species selection when both processes operate steadily and unidirectionally—for if both levels work in the same direction, then species selection can only add a small increment to the vastly greater power of organismic selection; whereas, if the two levels work in opposite directions, organismic selection must overwhelm and cancel the effect of species selection.

But the empirical record of most of the well-documented fossil species affirms stasis throughout the geological range (Eldredge & Gould 1972; Stanley 1979; Gould & Eldredge 1993, and references therein). The causes for observed nondirectionality within species are controversial, and the phenomenon is by no means incompatible with the continuous operation of strong organismic selection—for two common explanations of stasis as a central component of punctuated equilibrium include general prevalence of stabilizing selection, and fluctuating directional selection with no overall linear component as a consequence of effectively random changes of relevant

environments through time. But the observation of general stasis seems well established at high relative frequency.

In this factual circumstance, as change does not generally accumulate through time within a species, organismic selection in the conventional gradualistic and anagenetic mode cannot contribute much to the direction of a trend within a clade. Change must therefore be concentrated in events of branching speciation, and trends must arise by the differential sorting of species with favoured attributes. If new species' generally arise in geological moments, as the theory of punctuated equilibrium holds (Eldredge & Gould 1972; Gould & Eldredge 1977, 1993), then trends owe their explanation even more clearly to higher-level sorting among species-individuals acting as firm entities with momentary births and stable durations.

Organismic selection may trump species selection in principle, but if change at speciation is 'the only game in town,' then a 'weak force' prevails while a potentially stronger force lies dormant. Nuclear bombs certainly make conventional bullets look risible as instruments of war, but if we choose not to employ the nukes, then bullets can be devastatingly effective. The empirical pattern of punctuated equilibrium therefore becomes the factual 'weapon' that overcomes Fisher's strong theoretical objection to the efficacy of species selection.

2. A LITERARY STATEMENT ABOUT THE TWO MAIN PROPERTIES OF HIERARCHIES

Our vernacular language recognizes a triad of terms for the structural description of any phenomenon that we wish to designate as a unitary item or thing. The thing itself becomes a focus, and we call it an object, an entity, an individual, an organism, or any one of a hundred similar terms, depending on the substance and circumstance. The subunits that make up the individual are then called 'parts' (or units, or organs etc. depending upon the nature of the focal item); whereas any recognized grouping of similar individuals becomes a 'collectivity' (or aggregation, society, organization, etc.). In other words, and in epitome, individuals are made of parts and aggregate into collectivities.

The hierarchical theory of selection recognizes many kinds of evolutionary individuals, banded together in a rising series of increasingly greater inclusion, one within the next—genes in cells, cells in organisms, organisms in demes, demes in species, species in clades. The focal unit of each level is an individual, and we may choose to direct our evolutionary attention to any of the levels. Once we designate any focal level as primary in a particular study, then the unit of that level—the gene, or the organism, or the species, etc.—becomes our relevant or focal individual, and its constituent units become parts, whereas the next higher unit becomes its collectivity. Thus, if I place my focus at the conventional organismic level, genes and cells are parts, while demes and species are collectivities. But if I need to focus on species as individuals, then organisms become parts, and clades are collectivities. In other words, the triad of part–individual–collectivity will shift bodily up and down the hierarchy, depending upon the chosen subjects and objects of any particular study.

This dry linguistic point becomes important for a fundamental reason of psychological habit. Humans are

hidebound creatures of convention, particularly tied to the spatial and temporal scales most palpably familiar in our personal lives. Among nature's vastly different realms of time, from the femtoseconds of some atomic phenomena to the aeons of stellar and geological time, we really grasp, in a visceral sense, only a small span from the seconds of our incidents to the few decades of our lives. We can formulate other scales in mathematical terms; we can document their existence and the processes that unfold in their domains. But we experience enormous difficulty in trying to bring these alien scales into the guts of or our understanding—largely for the parochial reason of personal inexperience.

We make frequent and legendary errors because we read the styles and modes of our own scale into the different realms of the incomprehensibly fleeting or vast. Geologists, for example, well appreciate the enormous difficulties that most people encounter in trying to visualize or understand the meaning of any ordinary statement in 'earth time'—that a landscape took millions of years to develop, or that a lineage exhibits a trend to increasing size throughout the Cretaceous period. We continue to make the damndest mistakes, professionals and laypeople alike. I have, for example struggled for more than 20 years against the conventional misreading of punctuated equilibrium as a saltational theory in the generational terms usually applied to such a concept in evolutionary studies. The theory's punctuations are saltational on geological scales—in the sense that most species arise during an unmeasurable geological moment (meaning, in operational terms, that all the evidence appears on a single bedding plane). But geological moments are thousands of human years—more than enough time for a continuous process that we would regard as glacially slow by the measure of our lives (see Goodfriend & Gould (1996) for an example). Thus, punctuated equilibrium represents the proper geological scaling of speciation in a few thousand years, not a slavish promotion of our concept of instantaneity to the origin of species.

As we misunderstand the scales of time, we fail just as badly with differing realms of size. Our bodies lie in the middle of a range from the angstroms of atoms to the light years of galaxies. Individuality exists in all these domains, but when we try to understand the phenomenon at any distant scale, we fall under the thrall of the greatest of all parochialisms. We know one kind of individual so intimately and with such familiarity—our own bodies—that we impose the characteristic properties of this level upon the very different styles of 'thingness' featured at other scales of size. This inevitable bias provokes considerable trouble, for organic bodies are very peculiar kinds of individuals; and very poor models for the phenomenon of individuality at most other scales.

The 'feel' of individuality at other scales becomes so elusive that most of the best exploration has been accomplished by writers of fiction, not by scientists. The tradition goes back at least to Lemuel Gulliver, who didn't range very widely from our kind of body and our norm of size, and has been best promoted, in our generation, within the genre of science fiction. Film has also become a powerful medium of exploration, perhaps best expressed in two 'cult' films, *Fantastic voyage* and *Inner space*, both about humans shrunk to cellular size and injected into the body of

another unaltered conspecific. This ordinary body becomes the environment of the shrunken protagonists, a 'collectivity' rather than a discrete entity—while the 'parts' of this body become individuals to the shrunken guests. When Raquel Welch fights an antibody to the death in *Fantastic voyage*, we understand how location along the triadic continuum of part–individual–collectivity depends upon circumstance and concern. A tiny, if crucial, part of my body at my true size becomes an entire and ultimately dangerous individual to Ms Welch at a fraction of a millimetre.

The parochiality of time has served us badly enough, but this parochiality of bodily size has, for two reasons, placed even more imposing barriers in our path to an improved and generalized evolutionary theory—a formulation well within our grasp if we can learn how to expand the Darwinian perspective to all levels of nature's hierarchy. First, we understand (often viscerally) what our bodies do best as Darwinian agents—and we then grant universal importance to these properties, both by denying interest to the different key features of individuals at other levels, and by assuming that our 'best' properties must, by extension, power Darwinian systems wherever they work. Our bodies are best at developing adaptations in the complex and co-ordinated form that we call 'organic.' Many evolutionists therefore argue, in the most constraining parochialism of all, that only adaptations matter as an explanatory goal of Darwinism, and that such adaptations must therefore drive evolution at all levels. I don't even think that such a perspective works well for organisms—surely the locus of most promising application (Gould & Lewontin 1979)—but this attitude will surely stymie any understanding of individuality at other levels, where complex adaptations do not figure so prominently. How will Dawkins ever appreciate the different individuality of species, where exaptive effects hold at least equal sway with adaptations, if he continues to view sequelae and side consequences as 'the boring by-product theory' (Dawkins 1982, p. 215).

Second, we don't comprehend the scale-bound realities of other size domains, and we err by imposing our own perceptions when we try to think about the world of a gene, or of a species. In one of the most famous statements of 20th Century biology, D'Arcy Thompson (1942, p. 77) ended his chapter 'On magnitude' (in his classic work *On growth and form*) by noting how badly we misread the world of smaller organisms because we are big and therefore live in gravity's domain (a result of falling surface/volume ratios as creatures become large, but not a significant feature in other realms of size). If we have so much trouble for extremes within our own level of organismic individuality, how will we grasp the even more distant worlds of other kinds of evolutionary individuals? D'Arcy Thompson wrote:

'Life has a range of magnitude narrow indeed compared to that with which physical science deals; but it is wide enough to include three such discrepant conditions as those in which a man, an insect, and a bacillus have their being and play their several roles. Man is ruled by gravitation, and rests on mother earth. A water-beetle finds the surface of a pool a matter of life and death, a perilous entanglement or an indispensable support. In a third world, where the bacillus lives, gravitation is forgotten, and the viscosity of the liquid, the resistance

defined by Stokes's law, the molecular shocks of the Brownian movement, doubtless also the electric charges of the ionized medium, make up the physical environment and have their potent and immediate influence on the organism. The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast.'

Once we become mentally prepared to seek and appreciate (and not to ignore or devalue) the structural and causal differences among nature's richly various scales, we can formulate more fruitfully the two cardinal properties of hierarchies that make the theory of hierarchical selection both so interesting, and so different from the conventional single-level Darwinism of organismal selection. The key to both properties lies in 'interdependence with difference,' for the hierarchical levels of causality are bonded in interaction, but also (for some attributes) fairly independent in modality. Furthermore, the levels all operate differently, one from the other, despite unifying principles, like selection, applicable to all.

(a) Selection at one level may enhance, counteract, or just be orthogonal to, selection at any adjacent level. All modes of interaction prevail among levels and have strong impact upon nature

I emphasize this crucial point because many students of the subject have focused almost exclusively on negative interaction between levels, albeit for a sensible and eminently practical reason. In so doing, they verge on the serious error of equating an operational advantage with a theoretical restriction, and almost seem to deny the other modes of positive (synergistic) and orthogonal (independent) interaction. Negative interaction wins primary heuristic attention because this mode provides our most cogent evidence, not merely for simultaneous action of two levels, but even for the very existence of a controversial or unsuspected level. If two levels work in synergism, then we easily miss the one we do not expect to see, and attribute the full effect to a greater strength than expected for the level we know. But if the controversial level yields an unexpected effect contrary to the known direction of selection at a familiar level, then we may specify and measure the disputed phenomenon.

In the example cited previously (p. 3), individual selection favours a balanced sex ratio, while interdemic selection leads to female bias in many circumstances. Our best evidence for the reality of interdemic selection arises from the discovery of such biases—not so strong as purely interdemic selection would produce (for organismic selection operates simultaneously in the other direction), but firm enough to demonstrate the existence of a controversial phenomenon. But if interdemic selection also worked towards a 1:1 ratio, we could attribute such an empirical finding exclusively to the conventional operation of organismic selection.

Negative interaction, however, does yield a distinguishing consequence to highlight this mode of interaction as especially important in the revisions to evolutionary theory that the hierarchical model will engender. In the conventional Darwinism of organismal selection alone, stabilities generally receive interpretation as adaptive peaks or optima, thus enhancing the functionalist bias inherent in the theory, and unfortunate in my

view. The only structuralist intrusion into this theme ordinarily occurs when we have been willing to allow that natural selection can't surmount a constraint—elephants too heavy to fly even if genetic variability for wings existed; insects confined to small sizes by the inherited *bauplan* of an exoskeleton that must be moulted, and a respiratory system of skeletal invaginations that would need to become too extensive at the surface/volume ratio of large organisms. But constraints in these cases are passive walls, not active agents.

The hierarchical theory of selection suggests a strikingly different and dynamic reason for many of nature's stabilities: an achieved balance, at an intermediary point optimal for neither, between two levels of selection working in opposite directions. Several important phenomena may be so explained: weak female bias as the negative interaction of organismal and interdemic selection (see above); restriction of multiple copy number in 'selfish DNA' as a balance between positive selection at the gene level, suppressed by negative selection (based, perhaps, on energetic costs of producing so many copies irrelevant to the phenotype) at the organismic level (Doolittle & Sapienza 1980; Orgel & Crick 1980). I also suspect that stable and distinctive features of species and clades often represent balances between positive organismic selection that would drive a feature to further elaboration, and negative species selection to limit the geological longevity of such 'overspecialized' forms. In any case, a world of conceptual difference exists between stabilities read as optima of a single process, and stabilities interpreted as compromises between active and opposed forces.

As an example of overemphasis upon negative interaction, Wilson & Sober (1994, p. 592) ask: 'Why aren't examples of within-individual (organism) selection more common?' They mention the most familiar case of meiotic drive, and then give the conventional argument for rarity of such phenomena: the integrity of complex organisms implies strong balance and homeostasis among parts; any part that begins to proliferate independently will threaten this stability, and must therefore be opposed by organismic selection, a force generally strong enough to eliminate such a threat from below (though terminal cancer may represent a Pyrrhic victory for cell-lineage over organismic selection).

If selection within bodies always opposes the organismic level, then we must predict a low frequency for the phenomenon, as evolution has endowed the organismic level with a plethora of devices for resisting such dysfunctional invasion from within. While I accept this argument for a low frequency of selection contrary to the interests of enclosing organisms, selection within bodies may be common when we include the other modalities of synergistic and orthogonal interaction. The most interesting hypothesis for extensive selection at the gene level, the notion originally dubbed 'selfish DNA' (Orgel & Crick 1980; Doolittle & Sapienza 1980), explains the observed copy number of much middle-repetitive DNA as a result of orthogonal gene-level selection initially 'unnoticed' by the organism, though eventually suppressed by negative selection from above when copies reach sufficient numbers to exact an energetic drain upon construction of the phenotype. In fact, organismic complexity might

never have evolved at all without extensive gene-level selection in this orthogonal (or synergistic) mode. For if we accept the common argument that freedom to evolve new phenotypic complexity requires genetic duplication to 'liberate' copies for modification in novel directions, then how could such redundancy ever arise if organismic selection worked with such watchdog efficiency that even a single 'extra' copy, initially unneeded by the organismic phenotype, induced strong negative selection from above, and got immediately flushed out of a population by a kamikaze-like organism?

Leo Buss (1987), in a fascinating book on the role of hierarchical selection in the phylogenetic history of development, makes a compelling case for the vital importance of both synergistic and negative selection between levels in the history of life, which he views largely as a tale of sequential addition in hierarchical levels—so that nature's current hierarchy becomes a problem for historical explanation, and not an inherent system fully present throughout time. Buss argues that synergism must fuel the first steps in adding a new level atop a preexisting hierarchy (for initial negativity with the previous highest level would preclude the origin of a new level). But once the new level achieves a tentative foothold, it stabilizes best by imposing negative selection against differential proliferation of individuals at the level just below—for these individuals have now become parts of the new level's integrity, and selection at the new level will tend to check any dysfunctional imbalance caused by differential proliferation below.

(b) Each hierarchical level differs from all others in substantial and interesting ways, both in the style and frequency of patterns in change and causal modes

Nature's hierarchy, for all the commonality of unifying principles (selection, for example, acting at each level), does not display fractal structure with self-similarity across level. As the theory of hierarchical selection develops, I predict that no subject within its aegis will prove more fascinating than the varying strengths and modalities among levels. Just as the study of allometry has discovered characteristic and predictable scale-dependent differences in the structure and function of organisms at strongly contrasting sizes—a prominent subject in biology ever since Galileo formulated the principle of surfaces and volumes in the early 1640's, and beautifully codified in D'Arcy Thompson's (1942) masterpiece of prose and concept, *On growth and form*—so too does individuality as a tiny gene imply substantially different properties for a unit of selection than 'personhood' as a large species or an even larger clade. Allometric effects across hierarchical levels should greatly exceed the familiar (and extensive) differences between tiny and gigantic organisms for two reasons. First, the size ranges among levels are far greater still. Second, organisms share many common properties just by occupying a common level of evolutionary individuality despite an immense range of size; but the levels themselves differ strongly in basic modes of individuality, and therefore develop far greater disparity.

This problem of allometric effects strongly impacts our struggle to formulate a hierarchical theory of selection.

Human beings are both evolutionary individuals and organisms—yet the equally well-defined evolutionary individuals of other hierarchical levels are not organisms. Unfortunately, organisms represent a special and rather ‘funny’ kind of evolutionary individual, imbued with distinctive properties absent from, or much weaker in, other individuals (at other levels) that are equally potent as evolutionary agents. But if we mistakenly view our own unique properties as indispensable traits for any kind of evolutionary individual—the classic error of parochialism—then we will devalue, or even fail to identify, other individuals defined by different properties, and resident at other levels.

Consider, for example, the difficulty we experience—despite our preferences for reductionism in science—in trying to visualize the world of genes, where nucleotides function as active and substitutable evolutionary parts, and where chromosomes build a first encasement, followed by nuclei and cells, with our body becoming a collectivity, whose death will also destroy any gene still resident within. Think of the initial resistance that most of us felt for Kimura’s neutralist theory—largely because we falsely ‘downloaded’ our adaptationist views about organisms into this different domain, where high frequencies of neutral substitution become so reasonable once we grasp the disparate nature of life at such smallness. And if we fare so badly in grasping this world of the tiny and immediate, supposedly so valued by our reductionist preferences, how can we comprehend an opposite extension into the longer life, the large size, and the markedly different character of species-individuals—a world that we have usually viewed exclusively as a collectivity, an aggregation of our bodies, and not as a different kind of individual in any sense at all?

I like to play a game of ‘science fiction’ by imagining myself as an individual of another scale (not just as a human being reduced or enlarged for a visit to such a *terra incognita*). But I do not know how far I can succeed. We are organisms and tend to see the world of selection and adaptation as expressed in the good design of wings, legs and brains. But randomness may predominate in the world of genes—and we might interpret the universe very differently if our primary vantage point resided at this lower level. We might then see a world of largely independent items, drifting in and out by the luck of the draw—but with little islands dotted about here and there, where selection reins in tempo and embryology ties things together. What, then, is the still different order of a world much larger and longer than ourselves? If we missed the strange domain of genic neutrality because we are too big, then what are we not seeing because we are too small? Our mortal bodies are like genes in some larger world of change among species in the vastness of geolo-

gical time. What are we missing in trying to read this world by the inappropriate scale of our small bodies and minuscule lifetimes?

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