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8 **Generativity, Entrenchment, Evolution, and Innateness: Philosophy, Evolutionary Biology, and Conceptual Foundations of Science**

William C. Wimsatt

This essay is part of a larger project to develop an account of the evolution of phenotypic structure that complements the account we have of genetic structure. As developmental genetics increasingly shows, understanding the developing phenotype and its environment is crucial to understanding gene action. This project turns pivotally on a strategy for reintegrating development into evolutionary theory, and it promises strategies for a variety of problems in the biological and human sciences that are not solvable or not easily accessible on the genetic approach. These include the question of how to generate an adequate model of cultural evolution—which must include or interface closely with a theory of cognitive development in the broadest sense, applying to all cognitive, conative, and affective skills, and the domains of their employment—and a new and importantly different approach to the phenomena that have motivated the innate-acquired distinction. Section 1 provides an orientation to the approach and to why what I call generative entrenchment is so important to a theory of evolving systems. In Section 2, I focus on the classical innate-acquired distinction and provide a new and richer account in terms of generative entrenchment of the phenomena invoked in its support. The new analysis is compared with traditional accounts of innateness as genetic or canalized. I conclude that the old innate-acquired distinction should be retired, but its conceptual niche is not dispensable and is filled fruitfully by the new concept.

1 The Evolution of Generative Systems

Optimal Design and Historical Contingency

History matters to evolution. It's not far wrong to say that everything interesting about adaptation is a product of selection for improvements in design, or of history, or of their interaction.¹ Gould has emphasized the role of contingency in evolutionary processes, arguing that minor unrelated “accidents” or “incidents” can massively change evolutionary history.² It seems plausible—indeed almost inescapable—to believe that a successively layered patchwork of contingencies has affected not only the detailed organic designs we see and variations between conspecific organisms, but also much deeper things—the very configuration and definition of the possible design space and the regions they occupy in it. Deep accidents from the distant past not only define the constraints of our current optimizations, but constraints on these constraints, and so on, moving backward through a history of the deposition of exaptive³ dependencies, which become framing principles for the design of successively

acquired and modified adaptations. Ecological past and present run on similar tracks: genetic events—mutations, segregation events, independent assortment, and recombinations in inheritance are the most commonly cited sources of contingency, but no less important are chance ecological events—meetings leading to matings, migrations, symbioses, parasitisms, and predations. As George Williams quipped in 1966, “To a plankton, a great blue whale is an act of God.” (Better design as a plankton cannot save it if it happens to be in the wrong place at the wrong time.)

But accidental or contingent events *needn't* leave visible historical traces much later. Most do not. Many are (1) not heritable, or even if locally heritable, are (2) averaged out—lost in multiple intersecting entropic processes. Also (3) “Noise tolerant” design—both of phenotype and of genotype—damps out many fluctuations, and biological processes are designed to be noise tolerant through diverse adaptations, ranging from third-position synonymies in the genetic code, diploidy, and alternative metabolic pathways for many critical functions, up through developmental canalization, growth allometries, bilaterally symmetric organs, and macroscopic regulatory features of individual physiology, to various mechanisms in social groups, breeding populations, ecosystems, and trophic levels. (4) Optimization also erases history on the evolutionary time scale: over time, changing adaptations to changing circumstances gradually erode and reconfigure everything which is changeable (this point can be argued in different ways: See e.g. Lewontin 1996 and Van Valen 1973). The closer you approach an adaptive peak and the longer you remain there, the less obvious is the path you took to get there—or at least so it seems.

To mark history, an event must cause cascades of dependent events which affect evolution. Some contingent events are massive, immediately marking diverse biotic and geophysical processes, like the “large body” impact or impacts recorded at the K-T boundary that extinguished the dinosaurs and most other species on earth and gave small mammals a chance. No surprise: such a massive cause *should* have had far-reaching effects.

Most “contingencies” start small—single-base mutations that initiate selective cascades of layered exaptations with divergent consequences. Oxygen production as a metabolic by-product in ancient plants presumably started small, but hardly any contingency has had broader or greater consequences for evolution, which it had by spreading as these plants succeeded and becoming a much larger process. As oxygen rose in concentration, this atmospheric poison was initially adapted to, and then eventually utilized by nearly all creatures throughout the animal kingdom, thereby driving an energetically richer metabolism. Small contingencies that leave a mark in evolutionary history do so by becoming larger—amplified by recurrent processes—for organisms through the process of reproduction.⁴

Cascading sequential dependencies also occur in each individual during development. These reflect an evolutionary history of contingencies, of exaptation layered upon exaptation, a history unique to, characteristic of, and divergent in different lineages. This is the architecture of adaptation. This creation of layered dependencies, the structure of the product, and measures of the degree of such dependencies I call “generative entrenchment,” or GE. GE is not limited to contingent events. Probabilistically common or inevitable “generic” events (Kauffman 1993) or even unconditional laws of nature can become generatively entrenched—deeply utilized or “presumed” in the design of adaptive structures (Wimsatt 1986; Schank and Wimsatt 1988). But generative entrenchment can also happen to arbitrary contingencies, rendering them more or less context-dependent adaptive necessities—all the more striking for their seeming arbitrariness. *GE is essentially the only way that such smaller contingencies have a reasonable chance to be preserved over long stretches of macroevolution. Drift alone will not suffice* (Wimsatt forthcoming). *We see evolution as a contingent process because of generative entrenchment.*

So these systematic effects—the structure of dependencies—can also have systematic evolutionary consequences. Developmental processes are the source of these patterns—they are what allows these contingencies to persist. Models of them can be used alone and in concert with evolutionary genetics to expand the compass of an evolutionary account. Their scope is nothing less than the dependency structure of our adaptations and heuristics. This approach can also inform cognitive development, cultural, technological, and scientific change, and aspects of the structure of scientific theories. An account of generative entrenchment should get at and facilitate theorizing about these contingencies and how they are preserved, elaborated, or modified in evolution and in development.

Generative Entrenchment and Developmental Perspective on Evolutionary Dynamics

Development was left out of the evolutionary synthesis. This is now increasingly perceived as a fundamental and crippling omission. In the so-called synthesis of the 1930s and 1940s genetics called the tune, and that omission partly reflects the then primitive state of developmental genetics. But accelerating progress there since the early 1980s is now articulating, with interests of paleontologists and macroevolutionists, an emerging multidisciplinary convergence within biology richly delineated (and in part engendered) by Raff (1996). Developmental geneticists look for invariant features of development in search of broadly important mechanisms. As molecular geneticists they also focus on the micromachinery of the expression of genes, both as these are articulated in development and at their patterns of distribution

across phylogeny. These mechanisms and patterns of distribution will reveal important things about how the detailed contingencies structure the architecture of our developmental programs, though not about why contingencies—rather than just *these* contingencies—should matter.

The very existence and *structure of dependencies* in developmental programs is the metacondition that makes contingencies (and history) important in evolution—these contingencies, or those of other interacting lineages. *Features (whether contingent or not) that accumulate many downstream dependencies become deep necessities, increasingly and ultimately irreplaceably important in the development of individual organisms. This causes them to be increasingly conservative in evolution, and this together with the inheritance of features down taxonomic lineages leads them to become taxonomic generalities of increasing scope, broadly represented across many organic types.*⁵ This basic fact has broad implications: models of these processes can go far in explaining the structure of change in adaptive generative structures, and they may often be able to do so without detailed dependency on the micromachinery if they can capture more abstractly the degree and character of these dependencies. As a measure of the magnitude and character of these downstream dependencies, generative entrenchment becomes a tool for theorizing about them.⁶

This need for integrating development into accounts of evolution is even greater for cultural evolution: there, it may be the easiest thing to get a handle on. In biology, the genetics is straightforwardly combinatorial and relatively accessible, has a stable architecture through successive generations, and is traditionally (though increasingly problematically) treated as inherited through a single channel—the germ line. The whole genome is inherited in one bolus at the beginning of the life cycle, so it seems that we can clearly specify the genetic complement at the start of life. Developmental interactions, by contrast, seem complex: they depend on a constantly changing context both within and external to the developing and increasingly large and complex organism, and they are hard to analyze. Thus we seek to trace the *genetic* architecture of evolution and development, hoping to bring its apparent clarity and stability to bear on the complexity of phylogenetic and ontogenetic processes. Thus the rising promise (and promises!) of developmental genetics.

But for culture, the glass is reversed: (1) despite the common talk of “memes,” there is no intra- or inter-organismal Mendelism for ideas, practices, norms, or any other of our artifacts, and (2) there is no “memome”: (a) no bolus of significant ideas transmitted at the start of life, and (b) no standard size and (c) no form for the cultural “memotype,” and (d) no standard “memetic” units. (3) The means of transmission for memes are varied and baroque, involving multiple complementary and conflicting channels, which (4) are acquired and act sequentially throughout the

development and life span of the individual. Moreover, unlike the biological case, (5) the transmission channels used for a given idea can change from one generation to the next.⁷ Worse still, (6) acquisition of specific ideas or practices modulate later receptivity to others, so (7) heredity and selection are interwoven throughout the periods of development and learning—that is for humans, throughout virtually all of the life cycle. They are not separable as we can presuppose when we construct population genetic models of evolution. The “internal” memetics for the combination of ideas—confounding as they do processes of cognitive development, selection, and heredity—are too complex for a simple algebra.⁸

Cultural evolution is supposed to be different because it is “Lamarckian,” but *these* problems—all embedded within that uninformative label (also critically reviewed by Hull 1988, pp. 452–458)—are what makes cultural evolution so profoundly difficult to theorize about. If we try to imagine constructing a multigenerational evolutionary computer simulation for culture, we find that almost everything we can safely treat as constants in biological models needs to be treated as variables—even from generation to generation. The resultant explosion in the necessary complexity of the model is daunting.

The situation is not totally impossible, however. We can learn a lot from various idealized limiting cases, if we look not for a single model but for a family of related models which together explore the behavior in question. (See e.g. Boyd and Richerson 1985.) We need to be aware in such modeling that some questions are likely reasonable ones to pursue at that level of coarse detail, but that many are not. The more recently explored individual-based modeling approaches, which allow both for complex behavioral rules and intrapopulation variability, should be increasingly widely employed in this area—as they have already in artificial-life models incorporating social interactions.

But there are other saving graces for culture, which I want to exploit: cognitive developmental interactions, whether invariant or context-dependent, are more accessible and public than their biological counterparts, since in mediating learning, and because they are culturally transmissible, they must interface richly with the external world. (1) The richness of our socially and technologically developed language, visual representations, skills, disciplinary knowledge, and our means for communicating these, provide much more sensitive probes for assessing the ontogeny of our knowledge and practices than we have for virtually any aspect of biological development. Every skill or discipline that has sequential dependencies for the order in which its components must be acquired provides potential tests for unraveling characteristics of our conceptual ontogeny. This is not seriously compromised if the necessities are contextual so long as their contextual dependencies can be specified. (2) Moreover,

for the most part these probes are accessible, and their effects understandable, in readily understood terms—the cognitive skills through which these developing skills are exercised. (Of course, one must understand and possess these cognitive skills to analyze the dependencies, so “good old-fashioned internalism” still has an important place in *this* socialized account of scientific change.) (3) And those elements of our skills and knowledge that are significantly anchored by their downstream dependencies should possess a stability over time that could allow them to serve the structuring functions for theory and observation that genes did in biology but which “memes”—given the complexities discussed above—cannot do for culture. These strategies for exploring the developmental structure of our knowledge, capacities, tools, and regulative norms have been applied only in cognitive developmental psycholinguistics and some other areas of early cognitive development, and even there not as richly as they can be. (Compare Rasmussen 1987 for rich and varied applications in biology.) There is much more to be done to expand and increase the effectiveness of their use.

Such advantages suggest that to further understand cultural evolution, we should get as much as we can out of modeling the structure of developmental processes. We should continue to study ideas using traditional narrative internalist methods for detailed accounts of the development of particular ideational lineages, both within and across individuals (ontogenies and phylogenies, respectively). Only with these methods can we deal with the conciliations and interferences between ideas sequentially acquired through individual ontogenies, and also with the phylogenies of socially held cognitive structures, be they norms, scientific theories, or practices. Or sometimes, the memetics of how individuals construct their various conceptual schemes may be left as a neuro-psycho-sociological “black box” for general models that emphasize transmission while exploring the epidemiological consequences of different social structures. We will need a variety of models that look at different aspects of the whole system and its parts with varying resolutions. Occasionally, as with our studies of Weismann diagrams (Griesemer and Wimsatt 1988), or Punnett squares (Wimsatt forthcoming-a), there are cultural systems of well-individuated units for which we can track the hereditary, developmental, and evolutionary details of the same case with relative ease and clarity. Both of these papers discuss the methodological advantages of such studies. If we are going to make progress in analyzing cultural evolution, we need to look for more of these sorts of systems.

Models that integrate development and evolution promise other analogies between biological evolution and scientific change (Wimsatt forthcoming-c). They can suggest foci where scientific changes are more (or less) likely; and they predict a pattern of scientific revolutions qualitatively reminiscent of Kuhn’s model, though postulat-

ing different causes. They can also provide a molar dynamics for such change and offer a new dynamical but generically Quinean, naturalistic account of the analytic-synthetic distinction. They give productive handles on the phenomena for which the innate-acquired distinction is invoked, and they also provide strategies for relating scientific and cognitive processes to biological development and provide broader views of the interaction of developmental and evolutionary processes. A developmental model of evolutionary change emerges both from observations common to the generation of any complex adaptive structure and from dependency relations arising from that process. *These processes are thus of great generality and must be features of any account integrating development and evolution.* I illustrate their import with an example from a different source—which can be taken either as concretely or as metaphorically as you like—in the next section. I return to provide a general theoretical account in the following section.

Engineering a Dynamical Foundationalism

Consider a common observation from everyday engineering. Trying to rebuild foundations after we have already constructed an edifice on them is demanding and dangerous work. It is demanding: unless we do it just right, we'll bring the house down and not be able to restore it on the new foundations. It is dangerous: the probability of doing just that seems very great, and there are seldom strong guarantees that we *are* doing it right. We are tempted to just “make the best of it” and do what we can to fix problems at less fundamental levels. Given the difficulty of the task this is not just back-sliding temptation, but usually well-founded advice. These are the phenomena to be explained and exploited. They are extremely general and have many and diverse consequences.

This is as true for theories or any complex functional structures—biological, mechanical, conceptual, or normative—as it is for houses. *This is why evolution proceeds mostly via a sequence of layered kluges.* It is why scientists rarely do foundational work, save when their house threatens to come down about their ears. (Philosophers like to mess around with foundations, but usually when working on someone else's discipline!) Neurath's image of this activity as one of rebuilding the boat while we're in it is heroic. (That's why the image is so powerful—it is not an activity one recommends lightly!) Actual revisions are preceded by all sorts of vicarious activity, and if we must we fiddle at all levels to make it work. We'd all prefer to redesign a *plan*, rebuild only after we're satisfied with the revisions, keep in touch during the reconstruction to deal with problems that inevitably come up, and move in only after the rebuilding is done or nearly so—complete with all sorts of local patches and in-course corrections. Jokes about construction projects executed by theoreticians or by

architects who never visit the building site are legion, a rich source of folk wisdom about the difficulties involved in foundational revisions, or in getting from new foundations to the finished product.⁹

This bias against doing foundational work if one can avoid it is a very general phenomenon. Big scientific revolutions are relatively rare for just that reason—*the more fundamental the change, the less likely it will work, and the broader its effects; so the more work it will make for others, who therefore resist it actively*. The last two facts are institutional, social, or social-psychological in character, but the first two aren't. They are broad, robust, and deeply rooted logical, structural, and causal features of our world—unavoidable features of both material and abstract generative structures.

It is also rare for individuals to undergo major changes in conceptual perspective later in life.¹⁰ It is common folk-wisdom that we get more conservative as we age. Behavioral and mental habits “build up,” “increase in strength,” and increasingly “channel” our possibilities and our choices. These marked metaphors delimit proto-theories likely to leave their issue in any future theoretical accounts because they reflect deep truths about the common architecture of our behavior. Related features permeate biological evolution even more strongly and deeply than the cognitive or cultural realms. Von Baer's “law” that *earlier developmental stages of diverse organisms look more alike than later ones* is broadly true (with some revealing exceptions). It is most fundamentally an expression of the evolutionary conservatism of earlier developmental features. More usually depend on them, and so mutations affecting them are more likely to be strongly deleterious or lethal. So they persist relatively unchanged.

Differential dependencies of components in structures—causal or inferential—are inevitable in nature. Their natural elaboration generates foundational relationships. *The rise of generative systems in which some elements play a generative or foundational role relative to others has been a pivotal innovation in the history of evolution*, as well as—much more recently—in the history of ideas. There are eminently good reasons that mathematics, foundational theories, generative grammars, and computer programs have attracted attention as ways of organizing complex knowledge structures and systems of behavior. *Generative systems would occur and be pivotal in any world—biological, psychological, scientific, technological, or cultural—where evolution is possible*. Generative systems came to dominate in evolution as soon as they were invented for their greater replication rate, their fidelity, and their efficiency. We must suppose that even modest improvements in them spread like wildfire.

The spread of the informational macromolecules, RNA and DNA, has been one of the most irreversible reactions in the history of life. It was followed by others.

Skipping to the cultural level, the invention of language, the advent of written and alphabetic languages, printing and broader literacy, and other means of improving the reliable transmission and accumulation of increasingly complex information should have spread rapidly, under suitable circumstances. Essentially from this perspective, Diamond (1997) attempts a global and integrated explanation of the rise and character of civilizations, providing a mix of contingencies and autocatalytic and hierarchially dependent processes virtually designed for analysis via generative entrenchment. Adaptations (beginning with agriculture) that allow and support growing population densities, cities, and role differentiation (and consequent interdependencies) play a central role and make GE inevitable. Many levels of adaptation, mind, and culture have yielded similar inventions—new generative foundations. Campbell (1974) distinguishes ten levels of “vicarious selectors”—all *prima facie* suitable candidates. In each case, a similar dominance and irreversibility, products of runaway positive feedback processes, result in a contingent—but once begun, increasingly unavoidable—freezing in of everything essential to their production.

Similar phenomena emerging across importantly different disciplines suggest a new attitude toward foundations and foundationalisms that has broader philosophical merit: traditional foundationalisms are too static and poorly adapted to our constant state of acquiring, confirming, and infirming plausible and usually effective beliefs. I’m interested in construction (of knowledge and adaptations), but less with traditional static issues of *in principle* constructibility than with dynamical issues of how differential *rates* of construction and reconstruction affect what we will find in the world and its stability over time. There are generalizable and important things one can say about such processes. The generative role of entities is important to whether we keep them around. Golden or not, if you like eggs, protect the goose! This generative role is central to explaining what changes and what remains the same, the magnitude and rates of change, and ultimately, the basic features of all of our generative structures.

Classical foundationalists had it half-wrong: generative foundations are *not* architectonic principles for a static metaphysics, epistemology, or methodology. But they also had it half-right: generative foundations *are* the deepest heuristics for a dynamic evolutionary foundation. Once in place, generative elements can be so productive and become so rapidly buried in their products that they *become* foundational and *de facto* unchangeable. I suggest that *foundations and foundationalisms everywhere—logical, epistemological, cognitive, physicalistic, cultural, or developmental and evolutionary—owe their very existence, essential form, motivation, and power to the invention and evolution of generative structures.*

Darwin's Principles Embodied: The Evolution and Entrenchment of Generative Structures

To appreciate the generality of this approach, consider an abstract characterization of evolving structures. We can look at entrenchment in static contexts, but we find that more theoretical power arises from the generative role of entities in the adaptive structure of replicating and evolving systems. This is because ultimately, in evolving systems, it *is* the generative role of elements that causes resistance of their changing. The anchoring against change in structures of widely used elements requires few assumptions

- (1) structures that are generated over time so they have a developmental history (*generativity*), and
- (2) some elements that have larger or more pervasive effects than others in that production (*differential entrenchment*).

Different elements in the structures have downstream effects of different magnitudes. The *generative entrenchment* (GE) of an element is the magnitude of those effects in that generation or life cycle. Elements with larger degrees of GE are *generators*. This is a property of degree. If we are going to consider evolving systems (where GE really begins to have bite), the structures must

- (3) have descendents that differ in their properties (*variation*),
- (4) some of which are heritable (*heritable variation*), and
- (5) have varying causal tendencies to have descendents (*heritable variation in fitness*).

With the addition of conditions (3)–(5), these structures satisfy the requirements for an evolutionary process—conditions baptized by Lewontin (1970) as “Darwin’s Principles.”

So why add conditions (1) and (2) to the widely accepted (3)–(5)? The reason is that *any nontrivial physical or conceptual system satisfying (3)–(5) will do so via causal (phenotypic) structures satisfying (1) and (2)*. Condition (2) is inevitably satisfied by heterogeneous structures: try to imagine a machine or system whose breakdowns are equally severe for each kind of failure, in any part, under all conditions. (There aren’t any!) Any differentiated (or nonaggregative) system—biological, cognitive, or cultural—exhibits various degrees of generative entrenchment among its parts and activities.¹¹ And if one could start out with a system that violates (2), with every-

thing having effects of the same magnitude, natural and unavoidable symmetry-breaking transitions in mutation and selection processes would be self-amplifying, pushing evolution toward systems which increasingly satisfy (2) (Wimsatt and Schank 1988). It is thus unavoidable that evolutionary systems satisfy (1) and (2). They will thereby develop, and if they can reproduce and pass on their set of generators, they will have a heredity. (This order is didactic, not causal: without a minimally reliable heredity, systems cannot evolve a complex developmental phenotype, but developmental architecture can increase the efficacy and reliability of hereditary transmission. Heredity and development thus bootstrap each other—as emerging genotype and phenotype—through evolution.) This requires only that generators retain their generative powers (in context, within a tolerable range) under a sufficient fraction of accessible small changes in their structure. (Qualifications here indicate trade-offs between relevant parameters of the process.) Then they will also show phenotypic variations which inevitably (by the logic of Darwin’s argument) yield fitness differences, natural selection, and evolution.

“Darwin’s principles” never mention genes; neither do the new additions. *This expanded list of conditions gives heredity and development without ever introducing the usual replicator-interactor distinction.* (Due to Hull 1980, the replicator-interactor distinction has since been widely adopted as the appropriate way of characterizing the genotype-phenotype distinction for the informational generalization of “genes.”) Instead, I would borrow Griesemer’s account of *reproduction*, which roots a conception of heredity within an account of evolution as a lineage of developments (Griesemer forthcoming-a,b) to facilitate the central reintegration of development into our accounts of the evolutionary process. Genes are agents in these stories (at least in biology) but they are not the privileged bearers of information; rather they are co-actors with the developing phenotype and its environment as bearers of relationally embodied information.¹² I proposed in 1981b (see also Callebaut 1993, pp. 425–429) that we could employ GE to individuate genes in terms of their heterocatalytic role—as it were, by their phenotypic activity—rather than bring in talk of copying (an abstraction of their autocatalytic role) as replicator-based accounts try to do. A new “heterocatalytic” account of (biological) genes consilient with this is richly elaborated by Eva Naumann-Held (1997).

Heterocatalytic gene-like things picked out by the GE criterion in biology would include some but not all genes, some things that are not genes, and most often, heterogeneous complexes of both. In some domains (like cultural evolution) gene-like things may be picked out by GE criteria where there is arguably *nothing* picked out by autocatalytic criteria, or more commonly, where autocatalysis is such a distributed and diffuse process that there seems to be no point to try to track compact

lineages through it. (How does a scientific theory make a copy of itself? *Very* indirectly!) Consider economist Kenneth Boulding's comment that "A car is just an organism with an exceedingly complicated sex life."¹³ Like a technological virus, it takes over a complex social structure and redirects the resources of a large fraction of it to reproduce more of its own kind. Indeed, our economic system has fostered an environment—a "culture dish" in which the invention, mutation, and expansion of such cultural viruses is encouraged, many environmentalists would say, until it has assumed cancerous proportions. (See also Sperber 1995.) Griesemer's account dovetails naturally with GE, and it was designed to do so.

But back to the consequences of GE: If an adaptive structure meeting (1)–(5) is even minimally adapted to its environment or task, then modifications of more deeply generatively entrenched elements will have higher probabilities not only of being maladaptive but of being *more seriously* so. These probabilities become more extreme—in the simplest models, exponentially so—either for larger structures (e.g., if they grow by adding elements downstream), or as one looks to more deeply entrenched elements in a given structure. Either change increases the degree of "lock-in" of entrenched elements.¹⁴ Crucial for cultural evolution is the large number of ways we have for modulating or weakening GE temporarily or for some purposes so we can (occasionally) make deeper modifications and get away with it (Wimsatt 1987, forthcoming-c). (Most of these ways for facilitating deep modification are not applicable for, or are present only in much weaker versions for, biology. Thus, as we already know—for this and several other reasons—cultural evolution generally proceeds much faster than biological evolution.)

Selection acts on the structures as a whole, so parts of an adaptive structure are inevitably coadapted to each other as well as to different components of the environment. So larger changes in this structure will have to meet more design constraints. Fewer changes will be able to do so. So ever-larger changes tend to have a rapidly decreasing chance of being adaptive. Mutations in deeply generatively entrenched elements will have large and diverse effects, and thus are much more likely to be severely disadvantageous or lethal. Simple analytical models (Wimsatt 1986) and more realistic structures and simulations of them (Rasmussen 1987; Schank and Wimsatt 1988; Wimsatt and Schank 1988) demonstrate that entities or their parts with greater GE tend to be much more conservative in the evolution of such systems.¹⁵ Changes accumulate elsewhere while these deeper features appear relatively "frozen" over evolutionary time. This is the basis of von Baer's "law." It is revealed in our models to be a probabilistic generalization: there are things that appear early and are not deeply generatively entrenched, and things that appear late

and are. But there are strong probabilistic associations between earliness in development and increasing probabilities of and degrees of generative entrenchment. (But these are *only* probabilistic, so Ariew's claim [this volume] that there are "innate" things late in development does not by itself provide a counterexample to this analysis. I mentioned such a case in my (1986): parental imprinting on their young complements the young's imprinting on parents in many social species, and this is clearly selectively important. Parents' divergent and complex later behavior toward their young is obviously strongly influenced by it, so it is obviously relatively deeply generatively entrenched even if occurring later in the life cycle. Such kinds of cases are dealt with particularly well on Mayr's (1974) analysis, and on this one.)¹⁶

So one should be able to predict which parts of such structures are more likely to be preserved and which are more likely to change—and over broader time scales, their relative rates of change—in terms of their GE. What kinds of structures? They could be propositions in a generated network of inferences, laws or consequences in a scientific theory, experimental procedures or pieces of material technology, structures or behavioral traits in a developing phenotype, cultural institutions or norms in a society, or the dynamical structures, biological and cognitive, driving cognitive development. This is a *dynamical foundationalism*, in which a larger generative role for an entity makes it more foundational (in role and properties), more likely to persist to be observed and (for some fraction of them), to grow. (And if the generatively entrenched thing is more robust than its alternatives [Wimsatt 1981a], it is more likely to have been there from the beginning, so it will appear to have an almost unconditional necessity.) Thus an element is foundational in terms of its dynamical properties; so *this* kind of foundationalism, far from being static, encourages and contributes to the study of processes of change—at all levels.

This model applies in diverse disciplines. Working in developmental genetics, Rasmussen (1987) used it to predict the broad architecture of the developmental program of *Drosophila melanogaster* from the effects of its mutants and comparative phylogenetic data. Schank and I have applied it to problems in biological evolution and development ranging from the architecture of gene control networks (1988) and the role of modularity in development (forthcoming) to the evolution of complexity (Wimsatt and Schank 1988). I reconsider below the traditional innate-acquired distinction (Wimsatt 1986). Crossing the disciplinary spectrum, Turner (1991) employed generative entrenchment to analyze the distinction between literal and figurative meaning. It also has powerful applications to the study of scientific change (Wimsatt unpublished; and partially described in: Callebaut 1993, pp. 331–334, 378–383, 425–429; Griesemer and Wimsatt 1988; Wimsatt forthcoming-a, forthcoming-c).

Since the generative form of adaptive structures affects the foci and relative rates of their evolution, and since evolution also acts on that form, one should be able to trace feedbacks from developmental pattern to evolutionary trajectory and back again, identifying pivotal points where relative stasis or elaboration can cause major changes in evolutionary direction. These are *second-order* effects. This gives “dynamical foundationalist” theories greater explanatory power than one might at first suppose. Campbell’s (1974) “vicarious selectors” have demonstrated abilities to create or make possible new effectively autonomous higher-level dynamics. (See discussions of conditions for “dynamical autonomy” in Wimsatt 1981a, 1994.) Thus perception (one of his vicarious selectors) plus mate-choice have created runaway sexual selection processes and other dynamics leading natural selection in new directions (Todd and Miller 1998). Many new directions similarly become possible with cultural evolution (Boyd and Richerson 1985). And these processes build upon and interact richly with each other. They are in part products of GE, and they provide both new opportunities for its action and occasions for its use as a tool of analysis. Applied to the evolution of cognitive and cultural systems, this perspective provides new ways of extending evolutionary epistemology with new predictions and explanations. Differences between these processes can affect how the model must be developed and applied, and the kinds of results expected. These two topics—differences by subject area in how GE models should be developed and the character and consequences of elaborating these second-order effects—provide many areas for further development of this theory.

2 Generative Entrenchment vs. Innate-Acquired

Developmental Constraints, Generative Entrenchment, and the Innate-Acquired Distinction

One of these second-order effects provides a strong basis for broader connections with other disciplines (Wimsatt 1986, unpublished, forthcoming-c)—a surprising match of various features of GE with a distinction commonly made in very different terms. The innate-acquired distinction originated in philosophy, beginning with Plato’s *Meno*, and it has been discussed there almost continuously since. It was exported from there to ethology as the latter emerged as a science, where it has generated as many quarrels as in philosophy and with equally inconclusive results. It has seemed both central and problematic for millennia. GE can be used to give a powerful analysis of phenomena that the innate-acquired distinction has been invoked to explain throughout its range in ethology, cognitive development, linguistics, philos-

ophy, and elsewhere. And it does so without making problematic assumptions that have seemed inextricably linked with the distinction. Furthermore, given the distinction's traditional connections with the relations between biological and learned (or culturally fostered) inputs to behavior, this domain of phenomena occupies a critical transition zone between "strictly biological" and cognitive and cultural processes of development. If any common theory is to provide insights for both biological and cultural evolution through consideration of developmental processes, surely it should have rich applications here. If I am right, the rich uses of "innateness" in philosophy and the ease with which they could be carried over into ethology is no coincidence. The uncommon two legs of this controversial distinction have a common root—just not the one so commonly supposed.

Suppose, roughly, that to be innate is to be *deeply generatively entrenched in the design of an adaptive structure—to be a functional part of the causal expression of that system, and a relatively deeper one upon which the proper operation of a number of other adaptive features depend*.¹⁷ I take the notion of adaptive design to be unproblematic—at least in biology and in the broadly naturalized half of psychology. My 1972 and 1997b give extensive analyses of the notion of function and of functional organization—the key ideas behind adaptive design—explicating both in terms of selective processes. I presuppose these analyses here without further comment. This move toward GE explains more of the criteria offered for innateness than any other analysis. (I have found twenty-eight criteria so far, including eight new ones predicted by this analysis.)¹⁸ Unlike other approaches, GE also provides its explanations in a theoretically unified fashion: it explains why the criteria hang together and why they *should* be criteria for these phenomena. One might think that to do so well the new analysis must be very conservative. Not so!

I first summarize some claims made for innateness in the philosophical tradition, and I then list and discuss most of the major criteria used by ethologists. (All twenty-eight criteria I have found, and my assessments of their import for the various analyses, are included in tables 8.1 and 8.2 at the end of the chapter.) With these as data, we can begin to see the strengths of the GE analysis of these phenomena.

Claims about Innateness from the Philosophical Tradition

The philosophical tradition has provided many claims about innate knowledge. Even as ethologists eschewed talk about knowledge and substituted talk about behavior, these claims left a lasting imprint on discussions of the innate-acquired distinction. When the criteria support different interpretations, I note alternatives with parentheses. Claims explicable on the GE account are marked by a bullet. Perhaps the claim which has seen the widest range of interpretations is:

- (P1) Innate knowledge is in some sense *prior* to experience.
- (P1a) Innate knowledge exists *prior in time* to experience.
- (P1b) Innate knowledge is a (logical, causal, epistemic, normal) *precondition* for experience.
- (P2) Innate knowledge is *independent of* experience.
- (?) (P2a) The *justification* for or *origin* of innate knowledge is independent of or different from experience.
 - (P2b) Innate knowledge is independent of any particular experience in that it is *invariant across different experiential histories*.
- (P3) Innate knowledge often arises as an effect of or is “*triggered by*” experience.
- (P4) Innate knowledge is knowledge of *general* truths.
- (P5) Innate knowledge is *universal*—every member of a given class (usually human beings) has it. (This claim is obviously related to claim (P2b) above.)
- (P6) Innate knowledge has a *generative role* in producing other knowledge.
- (P7) Innate knowledge is often said to be different from other knowledge in being *analytic, necessary, or a priori*. (The first two relate to claim (P2a), above, and the last either to (P1b) or (P2a).)

Variations of these claims have been made in many combinations by many philosophers. I skirt over subtleties, seeking only to indicate the origins of ideas that have influenced more recent linguists, psychologists, and biologists in the philosophical tradition, which has midwived so many sciences and scientific concepts. In moving from that tradition to modern ethology, two major points are obvious and a third merits special mention:

- (1) Although many ethologists ascribed a mental life to at least the more complex animals they studied, they have avoided ascribing linguistic or conceptual knowledge (or the consequences of either) to them. This reflects the power of skepticism in Western philosophy since Descartes: it was worth doing battle with skepticism (or its cousin, behaviorism) for human knowledge, but ethologists seem to have capitulated and dropped at least the fourth and seventh criteria for animals. (If animals have any knowledge, it was assumed to be too low-grade to be general. Properties ascribed by (P4) and (P7) appeared to require too rich a mental life.)¹⁹

(2) Almost all criteria for innateness urged by ethologists relate to one or more of the above philosophical claims, appropriately transformed for the study of animals, as we will see in the list of ethological criteria below. So *behavior* or morphology was said to be innate, but not knowledge. Criteria (P1a) and (P2b) were carried across essentially unchanged but interpreted as comments about development (E2 and E1). (P1b) has an interpretation deriving from deprivation experiments, in which deprivation of a kind of experience (particularly early in development) produces loss of a *capacity* for later acquiring or interpreting a related or broader class of experiences (E8). (P2a) has an analogue in criterion (E6) below, suggesting different sources for innate and acquired information. (E4) is a richer version of, but still related to (P3). The criterion of universality, (P5), was split into two, reflecting evolutionary taxonomy: Universality within a species was taken as central (E1), and presence of a trait in phylogenetically related species as less so (table 8.1, no. 3)—an indirect indicator of a genetic basis for the trait.

(3) Surprisingly, the generative role for innate knowledge (P6) was ignored by most ethologists. It is not unconnected with the other philosophical criteria. (Thus it could give a reason for making claim (P1b), if either innate knowledge was *required* to produce other [experiential] knowledge, or [as a weaker “precondition”], if the latter were *characteristically* produced via employment of innate knowledge. As we will see, (P6) has close connections with most of the ethological criteria listed below—including some that are hard to explain without it.) This criterion was not ignored by Chomsky; generative role is central to his analysis—see his debate with Putnam (Chomsky 1967; Putnam 1967). Even though ethologists noted that some behaviors (including the ones they picked out as innate) played an important role in generating or engendering other behavior, they did not connect this directly with innateness—most likely because *innateness was seen as related to the origins or causes of knowledge or behavior, rather than as deriving from the effects of having or exhibiting that knowledge or behavior*. But generative role is the *most* powerful fulcrum in analyzing the relation between what have been called innate and acquired elements of behavior *and* knowledge. It is at the core of the analysis I give below.

Claims for Innateness in the Ethological Tradition

I now consider some of the standard claims made for innate behaviors. Each claim below is followed by comments on how (or whether) it is explained or predicted on the the two standard competing accounts of innateness, and how it fits with my GE account. The “genetic” account holds that something is innate if it is “coded in the genes”—a widespread and apparently intuitive locution, the consequences of which

are quite unclear as we will see. Lorenz sometimes (e.g., 1965) speaks as if this is what he means. The “canalization” account fits better with many of the claimed criteria for innateness (including other statements by Lorenz in the same book): it holds that innate traits are developmentally buffered, so that they appear in a variety of different environments. (See, e.g., Waddington 1957; Ariew 1996 and this volume.) Not claimed in Ariew’s formulation of this account (but required if it is to fit some important intuitions about innateness) is *genetic* canalization—the tendency for the trait to appear in a wide diversity (i.e., almost all) different genotypes for that species (The idea of genetic “homeostasis” or canalization was first systematically argued by Lerner 1954.)

One other point is worth noting in evaluating the accounts: does an account explain the criterion directly (as is commonly so with the GE account) or does it require additional hypotheses? (In the latter case it seems fairer to claim that the account is *consistent* with the criterion, or more charitably may even suggest it, rather than explaining it.) It is surprising how often subsidiary hypotheses are needed for either the canalization account or the “genetic” account to do their jobs. (These relationships and how they stand with the three different analyses are tabulated for the twenty-eight criteria in tables 8.1 and 8.2.)

The ethological criteria follow:²⁰

(E1) *Innate behavior for a given species is universal among normal members of that species in their normal environments.*

(E1a) On the “genetic” account, (E1) is taken to indicate that the innate behavior has a genetic basis. (But to get this universality we must also suppose that the relevant genes are fixed and that they have high penetrance—that they are virtually always expressed. These subsidiary hypotheses used to be common, but they are rarely defensible.) Talk of “high penetrance” also conceptually moves toward the canalization or GE accounts.

(E1b) On the “developmental” account, (E1) is taken to indicate that the innate behavior is “canalized” or homeostatically regulated so it appears in a range of environments (though given the genetic variability common in virtually all species, *genetic* canalization is also required for universality across the whole species. Ariew actually denies that species-typical universality is required, but he goes against many or most writers in doing so.)

(E1c) One the GE account (E1) follows directly: strong stabilizing selection produced by the number of other traits depending on the given trait’s normal expression guarantees both the universality of the trait and that any species member lacking it

will appear strongly abnormal. In addition, it is often adaptive for a generatively entrenched feature to be both genetically and environmentally canalized, so *we should expect that the second and third analyses will often be satisfied together.*

(E2) *Innate behavior appears early in development before it could have been learned, or in the absence of experience.*

(E2a) On the “genetic” account this is (incoherently) taken as a basis for saying that it is “more genetic,” because the environment will have had less time to act. (Note that on any realistic dynamical account of gene action, *the genes* will also have had less time to act!)²¹

(E2b) This feature is *not* predicted or explained on the developmental canalization approach, which has no resources for handling it. (Ariew denies that this feature is important, but again he thereby puts himself at odds with most writers. Indeed, this is one of the most firmly anchored intuitions that people have about innateness, and it would be nice to be able to capture it.)

(E2c) Traits expressed early in development are more likely to have high GE, so the association of (E2) follows directly, though without invoking “absence of experience.” This is a characteristic tendency, but contrary to Ariew’s suggestion, appearance early in development is neither necessary nor sufficient for a high degree of GE. There can be both highly generatively entrenched things late in development (recall parental imprinting on offspring), and low or even non-generatively entrenched things early in development—for examples any synonymous or neutral mutation, or “silent” gene.

(E3) *Innate behavior is relatively resistant to evolutionary change.*

(E3) can be explained only on the GE account, from which it follows directly, or (less successfully) on the developmental fixity account (if we assume genetic as well as environmental canalization and strong stabilizing selection. But the last comes close to assuming high GE). It could also be explained on the genetic account with the (for it) arbitrary assumption of stabilizing selection.

(E4) *Critical periods for learning certain information, or unusually rapid or “one-shot” learning, indicates the presence of an “innate teaching mechanism.”*

This, with E2 above, is the basis of Chomsky’s “poverty of stimulus” argument against behaviorist theories of language learning. It shows obvious generativity and so fits neatly with the GE account. Critical periods (e.g., for parental imprinting on young) can occur late in development. They seem less well accounted for by canalization

(which gets less explanatory the more complex the generated behavior—as I will explain below), and not at all on the genetic account.

(E6) *Innate information is said to be “phylogenetically acquired” (through selection) and hereditarily transmitted; acquired information is said to be “ontogenetically acquired,” usually through some variety of learning.*

Cited often as a criterion, (E6) seems to be used just as a restatement of the genetic criterion. It is also explained (and becomes a distinct though derivative criterion) on the GE account, since traits with high GE are overwhelmingly likely to be phylogenetically old. One could argue similarly (but less convincingly) for a canalized trait.

(E8) *Relatively major malfunctions occur if innate features do not appear or are not allowed to develop.*

(E8) is a direct and important consequence of the GE account, and it is not explicable on either canalization or genetic accounts without additionally supposing GE. It is actually characteristic of all paradigmatic cases of innateness, but it is surprisingly rarely mentioned as a criterion—though it does crop up in Lorenz’s (1965) discussion of the deprivation experiment.

In addition, since the rise of genetics and the modern synthetic theory of evolution, two new criteria have been added, presumably because they are criteria for a trait’s having a genetic basis:

(E9) *If a trait shows simple (e.g., Mendelian) patterns of inheritance, it is innate.*

This violates E1. If a trait is showing Mendelian patterns of inheritance, it must be segregating in the population. But then it is not invariant for that species—different variations normal for that species in environments normal for that species are producing different phenotypes for that trait.

(E10) *If a trait is modifiable through selection, it is innate.*

(E10) has the same problem as E9, though it also violates E3. Meeting this criterion would be doubly problematic for a GE trait, which would be very difficult to modify through selection because of E8. Note that on the GE account, selection is very relevant to the trait but selection is stabilizing, so for a deeply entrenched trait, that trait is not significantly modifiable through selection.

The last two criteria, (E9) and (E10), are of relatively recent provenance (since Mendel and Darwin, respectively). They were likely both added (see e.g. Mayr 1974)

as criteria for a trait having a genetic basis *on the assumption that “genetic” was the appropriate gloss for innateness*. Neither fits well with either the canalization or the GE account. Both conflict with (E1), and (E10) also conflicts with (E3) and (E8). So one can’t consistently maintain that all of (E1) through (E10) are criteria for the same concept. So perhaps there are two different concepts of innateness. Lehrman (1970) does essentially this—in effect individuating “genetic” and “developmental” senses of innateness, the second much as on the canalization account. But he rejects the developmental sense, interpreting the genetic (which he embraces) in terms of heritability. This move produces other problems, as Ariew (1996) shows nicely. I urge that on *any* analysis of innateness, these two criteria, (E9) and (E10), be rejected—at least in their present forms. Their intuitive fell has to do with their association with genetics. (I discuss the case for a distinct genetic concept of innateness in Wimsatt forthcoming-c: It adds nothing to saying that a trait is genetic. [I also discuss what it gives you to say a trait is genetic]. Furthermore, confusion of a supposed genetic sense of innateness with the quite distinct implications of the sense discussed here is responsible for many of the socially repugnant inferences drawn using that concept.)

A Comparison of the Generative Entrenchment and Ariew’s Canalization Accounts

Many features of the GE account have already emerged. The GE analysis has numerous other interesting features, most already noted in (Wimsatt 1986). Some of them follow:

- (1) GE is a degree property—widely acknowledged (since Lehrman 1970) as desirable on any acceptable analysis. (It shares this with Ariew’s account.)
- (2) GE captures (E2) (earliness in development), (E4) (critical periods/poverty of stimulus), and (E6) (ontogenetic vs. phylogenetic acquisition), which have been paradigmatic claims for innateness, but which the canalization account fails to do or does poorly. It captures (E2) and (E6) in radically different ways than traditional analyses, but this is a strength because it thereby avoids other serious problems with these accounts. One of these is the following:
- (3) By not trying to construe innateness as something that is there before learning, GE avoids problems traditional nativists have had with trying to say what learning is and when it begins, in a way that would allow them to distinguish learning from interactions necessary for development. (Development and learning surely fall on a continuum in many respects.) This cluster of issues have probably been *the* most problematic one for the nativist tradition.
- (4) Criterion (E8) (deprivation yields major malfunctions) often comes up in discussions of innateness but rarely criterially, and it is often ignored (but see Lorenz’s

1965 discussion of deprivation experiments). It assumes center stage on the GE account, which actually gives a better account of disturbances of normality and why these should be relevant than any other account. On the GE account (E8) also plays a role in explaining why (E1) (species universality) and (E3) (evolutionary conservatism) are met. As Griffiths (1996) points out, through it GE also provides room for a modest and qualified essentialism. Because of the causal importance of a generatively entrenched trait, anything lacking it (even if viable) will characteristically be seriously (and deleteriously) abnormal.

(5) This new analysis of things we have thought of as innate shows that they are intrinsically relational and connected with their environments in ways not captured by prior accounts. The equation of innate with genetic is ill founded—being genetic is neither necessary nor sufficient for being innate. (Equating “innate” with “genetic” is a kind of functional localization fallacy—assuming that the function of a larger system or subsystem is realized completely in a part of that system. Writers on developmental systems theory [Oyama 1985; Moss 1992; Griffiths and Gray 1994] have argued this effectively and at length.)²²

(6) Nor does it follow any longer that what is innate must be internal to the system. This follows from the relational character of the analysis. *Environmental* features could with equal justice be viewed as innate (Wimsatt 1986)—though neither should, properly speaking: treading carefully here would attribute innateness to the whole relationship. What is innate if anything is most fundamentally *relationships between phenotype and environment that serve to secure and increase fitness and its heritability*.

(7) The GE analysis turns traditional accounts on their heads in another way: the status of something is determined not by where it came from (the ethological distinction between phylogenetically acquired and ontogenetically acquired information) but in terms of its effects—its generative power. Generative power also allows generative linguists to invoke generativity without making claims that are developmentally and evolutionarily unsound. What is profoundly surprising is that so major a conceptual rearrangement can nonetheless capture so many of the traditional intuitions about innateness.

Ariew’s analysis of innateness in terms of developmental canalization is a reasonable reconstruction of an important (arguably, the single most important) recognized theme in discussions of innateness. I agree with much of his analysis, as far as it goes. Lehrman (1970) individuates two strands in Lorenz’s concept of innateness: developmental fixity (or invariance) and heritability. Unfortunately Lehrman embraces the second (Wimsatt 1986). Ariew and I would agree that fixity is more important, and we both make use of it, Ariew as the core of his analysis and I as an

important consequence of mine. We agree about many other things. His adequacy conditions are sensible: an acceptable account of innateness should make it a feature of development; it should involve or explain environmental invariance or stability; and it should make it clear how innateness is relevant to selection. Our analyses both satisfy all three of these conditions, though in different ways. He later lists a fourth desideratum—that innateness should be a degree property—which canalization and generative entrenchment accounts also both satisfy.

We differ in some other important respects, however.

(1) Ariew argues that various other accounts (including mine) face counterexamples, and thus should be rejected. But he himself chooses to ignore many criteria that have been offered for innateness—without offering (at least in his 1996 or his paper in this volume) any argument for doing so. Most striking of these are (E2) earliness in development, (E1) invariance in normal members of the species, and (E4) the emergence of complex behavior from simple stimuli. These criteria could easily be used to generate counterexamples to Ariew's account. I'll discuss the last of them further below.

(2) Ariew seeks an economical definition, and he sees no reason to consider every criterion one might find for innateness, perhaps believing that many of them are redundant or mistaken. I have taken a more inductive approach to the problem. It seems more appropriate to the special features of this case: a review of the literature shows a large number of criteria offered or in use—many more than Ariew considers. They are not all mutually consistent, so no account can meet them all. But this fact compromises the value of individual counterexamples (including those Ariew provides) unless there is a more systematic way of deciding which ones *should* count. How should one proceed? One can take several considerations into account in evaluating alternative analyses:

(a) Require that the analysis be consistent with and, if possible, relate to current theories of evolution, development, and heredity. (I will suppose that Ariew's and my account fare equally well here. Traditional nativist or genetic accounts do not. In fact, traditional genetic accounts are not consistent with modern understandings of genetics.)

(b) Try to find the largest consistent subset of criteria. (But this suggests taking the larger sample of my strategy, rather than starting with just a few!)

(c) If there are to be many criteria, look for an account that integrates those that are accepted, explains why they should be criteria for innateness, and gives reasons for rejecting others. (I think that the GE account does remarkably well at this, far better than any other account, including the canalization one.)

(d) Look at how directly the accounts explain the relevant criteria, and how many subsidiary hypotheses are needed to make the explanations work. A generation ago (before the discovery of widespread genetic variation for “wild-type” traits; the ubiquity of epistasis; and the emerging complexities of gene action) the genetic account would have appeared to fare much better, but many of its presuppositions have since been falsified. And (largely because he avoids *genetic* canalization, and because many of the effects of canalization emerge from its commonly coincident generative entrenchment) Ariew’s development of canalization often needs subsidiary hypotheses to meet the criteria. GE again does uncommonly well, in part because its effects are robust.

(e) Given that current “ethological” accounts of innateness are thinly veiled transformations of earlier analyses or criteria derived from the philosophical tradition, try to find an account that respects that tradition. (Again, GE seems to score much higher on this than any of its competitors. Ignoring earliness in development and species invariance costs Ariew here, but the GE account does far better than any of the ethological accounts in capturing²³ essentially all of the claims made about knowledge—i.e., even those ignored in the move from philosophy to ethology—in circumstances where talk of knowledge is appropriate. That is, the deeply entrenched claims in a conceptual structure are those that seem most general, abstract, analytic, a priori, and necessary. (Wimsatt unpublished, forthcoming-c; Turner 1991; Griesemer and Wimsatt 1988; Griffiths 1996.) And as Griesemer and I show, these features are characteristic not only of propositional structures, but also of the canonical representation forms that develop in lineages of widely used diagrams.

I have found an account that satisfies Ariew’s adequacy criteria and also meets the five preceding desiderata. It provides a single mechanistic account that exploits robust features of development and evolution to explain an unprecedented number of criteria for innateness better than—indeed *much* better than—any of the analyses that have been offered.

There is a price, however—GE violates some deeply held assumptions about innateness: characterizing a trait as innate in virtue of its consequences rather than the character of its causes; uncoupling innateness from genetics, and from being internal to the system. How fundamental can you get? Of course, none of these associations is denied simpliciter—each can be given a convincing gloss for why we should have believed it to be true. But this violation of deep assumptions alone might seem to make the inductive strategy essential: overwhelm the unintuitive character of the analysis by showing how many distinct criteria it explains. And that is surely an important power of the GE account, one which would not be apparent if we looked

at just a few criteria. But the inductive strategy was not invented for this purpose; I was impressed that there were so many criteria, some of them quite diverse. I had thought it quite likely (following Lehrman 1970) that *at least* two senses were involved, and I wanted to get a sense of the whole range of claims made for innateness before attempting to construct an analysis. I was quite astounded that so many of the criteria (and now I draw from the 7 philosophical criteria (P1)–(P7) listed earlier) as well as the twenty-eight ethological and evolutionary ones listed below in tables 8.1 and 8.2) could be captured as consequences of a simple mechanistic analysis that turns on basically one criterion with a few appropriate qualifications.

The GE account is so radically different in approach that it is tempting to describe it as an eliminative account, but if so it is one with a difference. Recent discussions of eliminativism in the philosophy of mind have been associated with threats to “urban renew” (i.e., bulldoze or demolish) our ordinary conceptions of “folk psychology,” replacing them with subpsychological concepts derived from theories of our neural hardware, whose conceptual basis would necessitate entirely new concepts at the macroscopic level. By implication, we would have to give up many or most of these folk beliefs as false. This has engendered various defenses of folk psychology arguing that we can’t do without these beliefs and that any possible conceptual revision that was adequate to the phenomena would have to preserve them in some form.

By contrast, *this* account of innateness is an eliminativist account that better and more richly accounts for and anchors the intuitive phenomena that innateness was invoked to explain than innateness itself. Because of this unusual collection of features, it may or may not technically be a better analysis of innateness as currently conceived than Ariew’s (though the criteria offered for it shouldn’t be irrelevant to this judgment!). In any case, GE seems both a better concept for organizing this domain of phenomena and better adapted to the future of theory in these areas. If any of the recent eliminativist theories of mind had even nearly the promise of this analysis of saving so many of the phenomena, they would never have been so roundly attacked.

A Closer Look at Canalization

Even if I urge a different account than Ariew’s (or Waddington’s), canalization is an extremely important concept, and it remains so both in developmental biology and in thoughts about the evolution of development. There is growing interest in this latter area concerning the experimental assessment of and conditions favoring the evolution of genetic and environmental canalization, and how they interact with each other, with stabilizing selection of different intensities, with inbreeding, and

with the evolution of modularity. (See, e.g., Stearns et al. 1995; Wagner et al. 1997; Rice 1998; Schank and Wimsatt forthcoming.) These kinds of studies and of the relation between canalization and generative entrenchment should be a natural outgrowth of growing interest in relations between evolution and development. I want to consider briefly (1) canalization's relation to generative entrenchment, and (2) its character as a phenomenological concept and its consequent plasticity for fitting a variety of diverse cases. The first emphasizes its importance for thinking about the evolution of development, and it helps to explain why canalization and generative entrenchment so often go hand in hand. The second suggests a dangerous looseness that is better avoided.

Relations between Canalization and Generative Entrenchment. Because canalization is a kind of regulatory phenomenon and because GE induces stabilizing selection for that feature, both can be expected to share sets of criteria in many respects. Indeed, one can wonder how many things quickly glossed as canalization instead reflect significant GE with at most modest canalization—as might be reflected in significant mortality of early deviant embryos, followed by modest regulation of smaller and later deviations. Nonetheless, GE and canalization are distinct—both as concepts, and also in the manner in which they are described. Waddington (and Lerner) characterize canalization phenomenologically, in terms of regulation of an outcome across environmental and genetic variation. This does not mean that one cannot do productive experiments or theory involving these concepts, but it does mean that there may be more play in how they are realized in any situation. GE is characterized more mechanistically, in terms of causal dependency relations in the production of phenotypic traits. This means that as we learn more about the mechanisms, the sophistication of our GE accounts, and what we can infer from them, will automatically rise.

It would usually be adaptive for entrenched things to be canalized: if it is strongly deleterious that an organism deviates from a state (whether static or developmental), it is advantageous to regulate its production as tightly as necessary to avoid deleterious effects, if that is possible (or to abort without expending further resources if not).²⁴ Thus one should expect selection for such regulation. In different circumstances, this might include some or all of environmental canalization, genetic canalization, and regulation of developmental trajectories (Waddington's 1957 *homeorhesis*, later assimilated to canalization.) (See Rice 1998.)

In yielding a stable state, canalization invites accumulation over macroevolutionary time of features that depend on that state. (See Wimsatt and Schank 1988 for elaboration of this argument.) Thus canalization breeds generative entrenchment.

(One can't come to depend upon things that aren't reliably there.) Stable states may become generatively entrenched, whether we think of them as internal or external. In perhaps the most extreme demonstration of this, Morowitz (1992) argues that primary metabolism is the entrenched remains of the prebiotic and early biotic "organic soup" in which life first evolved. In subsequent evolution, the external environment was materially internalized, becoming the "milieu interior" to control and regulate diverse organisms' entrenched states and to permit reliable and efficient operation of the processes that depended upon it.

Given that either canalization or generative entrenchment will under a wide range of circumstances favor selective enhancement of the other, we need to be very careful in analyzing cases that purport to explain innateness in terms of one while denying the need for the other. If evolution naturally builds organisms which have both it may be all too easy to utilize the properties of the "silent partner" while making the argument for the preferred criterion. Canalizations and generative entrenchments have obviously been interleaved many times in constructing our layered architecture of kluged exaptations. In the next section we will see various cases where canalization and generative entrenchment are almost inextricably interdigitated.

On the plasticity of canalization. Canalization is a phenomenological concept, suggesting a kind or kinds of developmental regulation without specifying any mechanisms for that regulation. Waddington (1957) explicates it with specific examples and the metaphor of the "epigenetic landscape"—in effect a kind of state-space representation for developmental trajectories, which I will return to below. Nothing in Waddington's characterization tells how wide or deep the regulatory channels ("chreodes") are, how they are determined, or how they are supposed to relate to intra- or interspecific differences. This then leaves lots of room for interpretation. One could imagine trimming the canalization "chreodes" quite narrowly, construing canalization as contextual, and avoiding "genetic canalization" by having the canalized states change with different genotypes within the species. We would then have different "innate" phenotypes for different genotypes, as Ariew apparently wants. Then innateness Mendelizes: one can speak of baldness and blue vs. brown eyes as innate traits, and criteria (E9) and (E10) are restored. This moves in the direction of merging the canalization account with the genetic.²⁵ But then it is not clear what function "innateness" serves that the term "genetic" doesn't already. It also then becomes only too easy to speak of innate intraspecific differences in all kinds of traits. But we've been there before, and it is dangerous and easily misused territory. Chomsky's scientific tastes for species-universals correspond with a good place to draw the distinction: keep innate differences at the species level or above. The GE

account goes even further, since it would start with a strongly winnowed subset of these species-specific traits.²⁶

Moreover, if we ignore genetic canalization and allow garden-variety intraspecific differences to be innate, it is hard to know how “phenotypic switching” could be easily included. With phenotypic switching, changed environments early in development yield characteristically and radically different adaptive phenotypes. Since the alternative phenotypes are significantly different, and since each appears to be relatively tightly regulated—one can’t easily generate a continuum between them—we have a threshold-based switching structure. Maybe one could say that their disjunction is canalized, but this begins to be a slippery slope away from environmental invariance and toward admitting almost anything. (Waddington 1957 had images of “nudging a ball” into one trough-trajectory rather than another in the “epigenetic landscape” with a small stimulus early in development: this fits developmental switching all right, but rather metaphorically, and it is hard to know how to explicate it without violating canalization. The problem is that the physical analogy suggests that it is the magnitude of the nudge, together with the height of the walls of the chreode (together with other issues such as the timing of events) that matter. But it is not the magnitude of the nudge that matters, but the character of the stimulus. Movement in the visual field works for greylag hatchlings, and conspecific cries do for other species, but nudges or hot breaths—two other forms of energy transfer—don’t work for either. Migratory vs. nonmigratory forms in locust species (Maynard-Smith 1975) and different morphs for caterpillars (Greene 1989) are mediated by phenotypic switching early in development in response to specific environmental stimuli that are good predictors of the environments in which the alternative phenotypes are better adapted. The bithorax response of developing *Drosophila* to ether in Waddington’s (1957) account of genetic assimilation (though maladaptive) and the Baldwin effect are reflections of this kind of sensitivity. This better fits a characterization of the system as a control structure with complex consequences that are both “programmed” and regulated. Neither term by itself is adequate. But the more structure there is to the consequences, the better the GE account fits, and the less revealing it is to claim that the behavior is canalized.

Another problem with this case for a “narrow” construal of canalization is that phenotypic switching is a species-specific characteristic that demands substantial *genetic* canalization because of the large genetic variability found in almost all natural species. If alternative trajectories and their environmental releasers were not stably present across different genotypes, they would never be recognized in nature as a stable response, could never serve their functions, and would never have had sufficient heritability to have evolved.

Couldn't one be a narrow canalizationist in some environments (to capture Mendelizing and selectable traits in natural populations and steal the ground from genetic accounts), a broad one in others (to capture species-universality and other macro-evolutionarily relevant criteria), and a structured one in still others (to capture phenotypic switching and all kinds of complex adaptive programmed interactions with the environment)? But how do we know when to be which? Without criteria to tell us we don't have an analysis that is of much scientific use. And notice that the second and third alternatives are each equivalent in different ways to sneaking generative entrenchment in the back door—for what else are the releasing parameters and the complex coordinated changes responding to them but rich programmatic structures whose architectures and characteristic responses are deeply generatively entrenched?

Part of the problem is that it is easier to start with a chosen "innate" trait and say how it is canalized or not, in what respects, and at what times in development, and how all of this may vary by genotype than it is to start with an idea of canalization and using just that criterion decide which traits are classified as innate. (All of the preceding qualifications then appear as gerrymandering, and the sense that one has captured the distinction seems to slip through your fingers.) To some extent, this can also be said for generative entrenchment, or perhaps for any category in a science with richly textured objects where a lot of the details matter—that is, at least for any evolutionary process. But I think that GE has more structure and seems much less prone to this problem than canalization.

A more diffuse but nonetheless serious problem for canalization is that it becomes less informative as an explanation the more complex and conditional the behavior becomes, whereas GE, with its invocation both of stabilizing selection and the accumulation of layered exaptations (which brings in seemingly arbitrary contingency) does successively better. The phenotypic switches discussed above, or the rigidly stereotyped mating rituals of various species, seem designed for a GE account. One might on a GE account expect evolution to produce a growing succession of initially arbitrary display, feeding, and appeasement behaviors which become added to differentiate rituals of closely related species. In these cases, it is obvious enough that the behavior is canalized, but also that it is generatively entrenched (both relative to the next part of the ritual and with respect to mating success). On the GE account, entrenched arbitrary contingencies (it doesn't matter what differentiates mating rituals in similar species that overlap, only that they be successfully differentiated) and the emphasis on dependency structure lead naturally to the complex interactions through which the behavior is realized—appropriately tuned to circumstance and the conventionalized offerings. Here the causal richness and environmental sensitivity of the adaptive design couples naturally with the definition of GE and its intentionally relevant causal dependencies.

Table 8.1
Standard criteria

Criterion for "innateness":	Import		Canalization G = genetic E = environmental		Genetic	Generative entrenchment	Comments:
	Import	Import for GE	G = genetic	E = environmental			
1. Developmental canalization or fixity	••	••	X		not implied	X	Defining criterion for "canalization" analysis (for "normal" members of that species) Treated as weaker "inductive" criterion Traditionally important, and common, but not necessary or sufficient on GE analysis Presupposed by Chomsky's "poverty of stimulus" argument Often ignored in analyses but crucial to Lorenz and pivotal to GE account From Lorenz's early "hydraulic" model Nativist counter to empiricism Contrasted with flexibility of learning Crucial for Ethologist's focus on behavior Contrast with S-R learning paradigm Connected w. poverty of stim. and imprinting Derived but important property of GE Not learned, thus innate (related to 5 above)
2. Universality within species	••	••	X (Ariew: no) (G ⇒ yes)		x (if fixed)	X	
3. Presence in related species	•	•	(G ⇒ more likely)		x	X	
4. Appears early in development or in naive individuals prior to opportunity for learning	••	••	no		no	X (conditional)	
5. Simple stimuli → complex char. behavior	••	•	(problematic)		X	X	
6. Deprivation → major malfunctions	••	•••	(possible: Canaliz. is often GE'd)		X	X	
7. Releaser elicits activity			yes?			(x*, case of #5)	
8. Teaching mechanisms are innate						X	
9. Stereotypy of behavior	•	?	X?		?	x*	
10. Parallels between behavior and phylogeny		•	(G ⇒ more likely)		?	X	
11. Unusually easy, rapid 1-shot learning	•	•	X			X	
12. Critical periods for learning	••	••	?			x*	
13. Resistance to evolutionary change		••	X?		X?	X	
14. Spontaneous prod. of complex behavior	•		homeorhesis (but problematic)			X	

15. Imprinting is irreversible	•	X	Lorenz 1937
16. Imprinting is not repeatable		X	Lorenz 1937

How different analyses of "innateness" deal with criteria or characterizations found in the ethological literature.

Relations between criteria and the specified analysis of innateness:

X = true by definition; X = presupposed by; X = explained by; x = consistent with; x = explained by with addition of subsidiary hypothesis;
 * = explicable with addition of Mayr's closed/open program distinction; blank = no relation claimed, but consistent with; "yes", "no" indicated explicit claimed connection or denial.

Importance of criteria: ●●● = ineliminably important ●● = centrally important; ● = important.

Table 8.2
Criteria demoted and new predicted criteria

Criterion for "innateness": denied or not central on ge analysis:	Import	Import for GE	Canalization	Genetic	Generative entrenchment	Comments:
17. I/A as phylogenetic/ontogenetic acquired	••		no	X	explicable but not central on GE	alt. characterization of I/A; Definitional? Q-able whether an independent criterion
18. Mendelian or other simple inheritance	?		possible if NO genetic canalization	yes	no	derived from "innate = genetic" equation Mayr: segregating behavior in <i>speckles</i> hybrids
19. (currently) selectable (\Rightarrow heritability $_ 0$)	?		yes	yes	no?	derived from "innate = genetic" equation?
20. (physical) modularity of functional trait	?				no?	emphasized by Chomsky, linguists, and no one else. [a mistake!]
Predicted on GE analysis:						
21. reappearance of early simpler (reflexive) traits after (brain) damage in adult	•				x	noted by Teitelbaum for rooting and grasping reflexes
22. phylogenetic ancestral traits in hybrids	•	•	X?		X	Darwin's argument that all pigeon varieties are descended from ancestral rock pigeon; relates both to canalization and to generative entr.
23. early devel traits more evol conservative		••			X	closely conn. w. GE and von Baer's "law."
24. deeply entrenched generative role	•	•••			X	defining criterion for "GE" analysis; generativity noted as important by Chomsky
25. existence of supernormal stimuli					X	like poverty of stimulus, a consequence of simplicity of releasing stimuli
26. analogies in cognitive structures	••				X	centrally important for "innateness" in mental., and philosophical origin of ethological concept.
27. restricted modes of deep GE modification		•			X	plausible consequence of GE for innateness
28. association between "habitual" & "innate"		•	no	no	X	vernacular: plausible on GE account, by analogy; contradicts genetic account

How different analyses of “innateness” deal with criteria or characterizations found in the ethological literature.

Relations between criteria and the specified analysis of innateness:

X = true by definition; X = presupposed by; X = explained by; x = consistent with; x = explained by with addition of subsidiary hypothesis;
 * = explicable with addition of Mayr’s closed/open program distinction; blank = no relation claimed, but consistent with; “yes,” “no,” indicated explicit claimed connection or denial.

Importance of criteria: ●●● = ineliminably important ●● = centrally important; ● = important.

Tables 8.1 and 8.2 include all criteria I have been able to find in the literature or in conversation with practicing scientists in the disciplines affected. Most are found widely in the literature, with 1, 2, 4, 5, 12 and 13 probably the most common. (I have not done a systematic census and tally). Most writers use multiple criteria, often drawing on more than they list explicitly. Thus Lorenz (1965) uses many of them seriatim in his discussions, either criterially or as comments about innateness, and has probably used or discussed almost all of the first 16 at one time or another. Mayr (1974) lists six explicitly, (10, 4, 9, 18, 19, 1), but I know no other sources listing nearly this many. The judgments of importance are not based on a systematic careful survey, but on lots of reading and talking with practitioners. Different individuals may weight different criteria differently—if I am right, indicating how much use they have made of them themselves and reflecting the role that generative entrenchment plays in their own thinking.

A final observation indicates the significant differences between the GE approach and either the genetic or canalization accounts. This is the natural association in common speech (no. 28 in table 8.2) between instinctive behavior and things that have become habitual—especially intentionally, through practice, and especially if done smoothly, or sometimes stereotypically. Thus, “on hearing the faint click, he *instinctively* went for his gun”—a plausible description in the middle of any “dime” Western. There are myriad varieties of this statement. It fits (at least roughly) criteria 5, 7, and 9 from table 8.1, but without satisfying either the genetic or the canalization accounts. It is complex behavior which must be learned, even trained for, which has become “chunked,” “black-boxed” (Latour 1987), or modularized. It cannot any longer be executed piecemeal, but only as a unit, and it must be started “at the beginning,” not in the middle—showing that its early pieces (and sometimes its learned “releasers”) are generatively entrenched relative to the rest. This example midwives the transference of the GE account from biology and developmental psychology to the unchallenged common minutia and practices—and the most deeply entrenched principles—of science and culture. But that is a story for another time.

Conclusion

Canalization seems an intuitive reading of much of what many past theorists (including Lorenz) have had in mind by innateness, though it fails to capture some crucially important criteria. GE provides an extremely fruitful reconstructive analysis which fits existing claims (including Lorenz’s) better than any other, offers new fruitful connections and predictions, is consistent with modern accounts of the relation between genes and development, and provides an engine for evolutionary change for the developmental systems view. Particularly intriguing (but only hinted at here) is the ease with which the GE account captures or explains many of the traditional philosophical criteria (P1)–(P7) for innateness. This suggests a fruitful naturalistic analysis of the a priori–a posteriori and analytic–synthetic distinctions, which I provide elsewhere (Wimsatt unpublished, forthcoming-c). Accepting the GE account requires breaking some strong associations made in traditional accounts of innateness, but it allows making many others in a satisfying and unitary fashion. Since no analysis can consistently capture all of the criteria, the loss of these associations should not be taken as critical. Perhaps in the long run they will be regarded as important only for helping to understand why this alternative powerful reading of the phenomena known as “innate” has remained invisible for so long. Finally,

the strongly relational character of this analysis can torpedo the basis for recurrent nativist claims that something is innate and therefore independent of environmental involvement or effects. It is time that we stopped basing faulty social analyses on mistaken conceptions of human nature anchored firmly in obsolete biology.

Acknowledgments

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Notes

1. I avoid talk of maximization of fitness or even constrained optimization of design here: satisficing accounts better fit available mechanisms (Simon 1982, 1996.) Analysis of population genetic models show that fitness is maximized only in highly idealized and notoriously limited circumstances—rarely if ever found in nature. Satisficers can use maximization accounts as heuristics to qualitatively identify possible attractors and to structure and conceptualize many problems, but this has no deeper significance. For a useful classification of such optimization methods in the related context of rational choice, see the introductory chapter in Gigerenzer, T. et al., 1999. See also Wimsatt forthcoming-b, ch. 1.

2. Evolutionary biologists use “contingency” differently than modern metaphysicians: the opposition is not between “necessary” or “analytic” vs. “contingent” (as possibly false), but law-bound or probable vs. unlikely or arbitrary. The distinction is not unlike Aristotle’s distinction between necessity vs. chance or accident.

3. Gould and Vrba (1982) define an exaptation as a feature of the phenotype that is not itself an adaptation (i.e., a product of selection for that feature), but which provides a base for the evolution of a new adaptation or function. After selection has elaborated this feature it has become an adaptation or a part of one. In emphasizing this aspect of evolution, Gould and Vrba wanted to emphasize the “fortuitous opportunism” and sometimes circuitous paths taken in the creation of adaptations.

4. This applies not only to the contingencies, but to their detection. If you find a fossil, even if it is the only known instance of its type, the chance that it *represented* a rare type in its time and place is small.
5. I do not suggest that elements cannot change earlier in development (they may be early without being entrenched, and some changes in them may be selectively neutral). Nor is it impossible to change deeply entrenched elements: it is more improbable, and changes must meet more constraints. Various mechanisms, both in biology and in culture, can make deeply entrenched change significantly less unlikely. Some such mechanisms *must* exist: Raff (1996) documents relatively common changes early in development (in pre-Bauplan stages) in some phyla and urges an “hourglass model” with variation necked at the Bauplan stage. And for scientific theories (which show many of the same patterns favoring conservation of deeper theoretical structures), many of the deepest structures of current theory date only to the last scientific revolution—so called for just that reason (Wimsatt 1987, forthcoming-c). Closer study of the nature and evolution of mechanisms permitting deep change (such as modularity—see Schank and Wimsatt 1998) is an important elaboration of this theory.
6. Interest in exploiting a GE-like perspective and in problems with similar characteristics is growing. These related ideas have been invented independently at least four times. (See Riedl 1978; Wimsatt 1981b; W. Arthur 1982; Glassman and Wimsatt 1984; W. Arthur 1984; Wimsatt 1986, unpublished; Rasmussen 1987; W. Arthur 1988; Schank and Wimsatt 1988; Wimsatt and Schank 1988; Turner 1991; Griffiths 1996; B. Arthur 1994; W. Arthur 1997; Schank and Wimsatt forthcoming; and Griesemer forthcoming-a,b.) In his rich review of approaches, Nelson (1998) documents an increasing number of attempts to move in this direction within paleontology and developmental biology over the last decade. Riedl (1978) is the classic first development of a theory of this kind. W. Arthur (1997) currently has the fullest account of generative entrenchment for evolution and development. B. Arthur’s (1994) work is having growing impact in economics and other social sciences. My further work on it (published and unpublished, in biology, cognitive development, cultural evolution, and scientific change) will be included in a book now in process (Wimsatt forthcoming-c).
7. This can actually happen in genetics, if a virus caught through normal epidemiological means leaves through its action a change in the germ line of its host. Some now think that this can be a significant cause of informational change over macroevolutionary time. Nonetheless, the relative frequency of such biological events is many orders of magnitude smaller than the corresponding cultural events would be. I ask my students to imagine what genetics would be like if we caught, in each generation, (an average of) half of our genome from viruses, and which viruses we had been exposed to affected our sensitivity to selected other families of viruses and modulated our behavior toward placing ourselves in situations where we could be infected (again by perhaps different specific families) of other viruses. This begins to suggest but does not exhaust the complexity of cultural transmission and evolution.
8. Many of these crucial differences are discussed—from a somewhat different perspective—in Boyd and Richerson’s pivotal review of the characteristics of cultural transmission in chapter 2 of their (1985). Their influence in this area is deservedly immense.
9. We *do* sometimes have to live in the house while it is being rebuilt. But this only works because the conceptual organization of science, and of engineering practice, is usually robust, modular, and local, each of which reduces GE. Shaking (local) foundations usually doesn’t bring the house down, and we still have a place to stand (on neighboring timbers) while we do it. For a sense of life at the critical edge (!) read Rhodes (1986) on revising theory and practice in the design, construction, and testing of the first nuclear reactor and atom bomb, or Feynman’s view (Gleick 1992) of the groping development of theory and computation at Los Alamos when they *had* to have accurate results without direct experiments.
10. Though his ultimate conclusion favors the account in terms of GE given here, Hull’s careful review, analysis, and discussion (1988, pp. 379–382) of “Planck’s Platitude” (that older scientists are slower to accept new theories) shows how dangerous easy generalizations are in this area.
11. On functional differentiation, aggregativity, and emergence, see Wimsatt (1997b), (1997a), and forthcoming-b, respectively.
12. There are more complexities to Griesemer’s story than I can address here, and it is much richer than my (1981b) proposal to define genes in terms of their heterocatalytic function, as is Naumann-Held’s. Griesemer argues that material transmission from generation to generation is a crucial feature of

reproduction—which may differentiate it from cultural transmission, with further interesting consequences. He also has many things to say on the distorted representations of the biology induced by the “informational” or “replicator” conception of the gene. Griesemer’s account is now getting increasing attention from well-known “gene-centered” biologists. Thus Szathmary and Maynard-Smith (1997) quote his account approvingly as delivering more clearly the conceptual revision they had sought.

13. From my notes of Boulding’s lecture at Max Black’s seminar in the “humanities, science, and technology” program at Cornell University, 1974–75. The following elaboration is mine, but Boulding got a widely appreciative laugh, indicating that his audience quickly drew just this interpretation.

14. “Lock in” is Brian Arthur’s (1994) term for the same process—which he explores in economic models of the development of technology, the formation of cities, and other cases where increased adoptions of an action or technology reduces the relative cost of doing so to others, generating a positive feedback loop. Arthur rigorously develops relatively simple models (usually with just two alternatives, and often with analytical results), whereas the work on GE has focused with less rigor on larger adaptive structures with greater differences in depth of GE, using simulations and qualitative discussions.

15. My first model of GE—the developmental lock—goes back to 1972, but it is not discussed in print until 1981b. See also Glassman and Wimsatt 1984, and Callebaut 1993.

16. Ariew suggests that the appearance of pubic hair is both late and innate, so thus a counterexample to the GE analysis. But it is not terribly late (appearing during adrenarche, in middle childhood), and it is clearly part of a very pleiotropic complex of activities initiated by adrenal hormones (DHEA and its products) playing an important role in the developmental emergence of sexuality. McClintock and Herdt (1996) show that sexuality starts earlier (at adrenarche, around age 10) than formerly supposed (at gonadarche, around ages 12 for girls and 14 for boys). Furthermore, mammals have a variety of social activities mediated by pheromone secretions, many from the regions of the secondary sex characteristics. (Odor plays a critical role in mating in many species. Its role in other behaviors is not denied, but simply unknown.) Chemical compounds emitted from the axillary (underarm) region in humans have recently been shown to speed up or slow down ovulatory cycles in other women as a function of when in the cycle they are emitted (Stern and McClintock 1998). The glands in this area as well as in the pubic and areolar areas complete development and become active as pubic hair emerges, and the hair follicles may be foci of secretion and the oily and curly form of the hairs may aid in their dissemination. This area of research is still relatively new (see news and views commentary by Weller in the same issue of *Nature* as Stern and McClintock), but it is at least as plausible at this stage to claim that pubic hair and the consequences of its emergence then are deeply generatively entrenched as it is to claim that they are not. Indeed, McClintock notes (personal conversation) that because many of these structures are already morphologically well developed in the fetus and in the neonate, they may well be deeply generatively entrenched in other respects.

17. Or it may be a relatively ineliminable consequence of such a deeply generatively entrenched trait. This qualification is required to deal with cases where an entrenched and adaptive trait may have maladaptive or nonfunctional side effects. This suggests that there can be such things as “innate” or “intrinsic” design flaws or limitations. And of course, in the real world, every design must make its compromises among conflicting design constraints and desiderata.

18. Conceptual analyses can make predictions just as theories can. A good analysis of a phenomenon will generate criteria in terms of some deeper understanding of its character, just as a theory of a mechanism can be used to generate good indicators of its presence. Test the analysis by asking knowledgeable observers what they think of the criteria. My new criteria are successful in this sense. See my (1986), (forthcoming-c).

19. (P4) is arguably false for an important subclass of cases in ethology: imprinting may be to an individual (parent or offspring) or a class (species-typical mating song). But (P4) and (P7) are captured at least qualitatively in applying a GE analysis to the analytic-synthetic distinction via a dynamical foundationalist analysis of scientific knowledge and change (Wimsatt unpublished, forthcoming-c; Griffiths 1996). The strong *cognitive* associations of the innate-acquired distinction persist: curiously, it seems never to have been applied to the behavior of plants—something neither predictable nor explicable on *either* Ariew’s analysis or mine!

20. This numbering follows Wimsatt 1986. (E5) and (E7) from that list are not discussed here, but appear as criteria 9 and 10 in table 8.1.
21. Among genes, maternal-effect genes fit this account best, acting before conception in the formation of the egg cytoplasm, or in placental mammals, in the embryo's environment. Maternal effects should be paradoxical on traditional "genetic" accounts of innateness because they are examples of extranuclear (and even extra-organismal) inheritance, and the genes are acting not in the offspring, but in the mother.
22. We have exploited the biases of the gene-centered perspective since early in this century. Its enormous inertia (generative entrenchment!) informs how we conceptualize all sorts of fundamental relationships in biology. We must stand outside it to see its limits (as developmental-systems theory does) to better assess its true strength. Many urge that the "innate-acquired" distinction simply be trashed. Productive thought in the new paradigm—or effectively avoiding the missteps of the old distinction—may require it.
- GE combines elements of genetic and selectionist theories in developmental form. It is essential to a developmental-systems theory, as the closest available thing to a motor that could drive evolutionary change. GE actually explains trajectories more in terms of highway construction than propulsion technology, but things that look like constraints or pathways on shorter time scales may act as generative motors on longer ones. But developmental-systems rhetoric is sometimes overstated: we should not hasten to reject genetic explanations, especially newer perspectives from developmental genetics: new theories must remain in contact with well-developed tools already in the discipline or be dismissed as obvious heresy or pointless unprincipled worry. But one can use these tools without regarding them as foundational. (Griesemer 1999a, 1999b is forging this as yet poorly marked path.)
23. Capturing or making clear why it should *appear* to capture—*pace* Hume on explaining our vulgar notions.
24. Like all "adaptive design" arguments, this requires detailed qualifications, which won't be provided here.
25. Mendel (1866/1902) made clear in choosing the characteristics for his experiment that he sought traits that were relatively insensitive to environmental conditions, so as to get clear ratios and avoid possible confounding effects of environmental variation. So he too made use of canalization. This was indeed an elegant aspect of his experimental design.
26. This is at least partially a tactical decision of how to draw the boundary, rather than simply of who is right and who is wrong. The issuer of where to draw boundaries is an unavoidable source of argument with a degree property. But as should be obvious, I favor the GE account over the canalization account for reasons stronger than tactics.

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