

# Chapter 3

## Robustness: Material, and Inferential, in the Natural and Human Sciences

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### 3.1 Robustness Introduced: Historical Background and Stage Setting

When I came to Chicago as a post-doc in the summer of 1969, to work with Richard Lewontin, I also met Richard Levins, a deeply reflective, politically active, and strikingly creative mathematical ecologist. Both were to have a deep influence on how I saw science. Levins was the author of a remarkable paper that I had read as a graduate student, published in *American Scientist* in 1966, “The Strategy of Model Building in Population Biology”. Among several other innovative ideas, sketched there and then further elaborated in his 1968 book, *Evolution in Changing Environments*, Levins proposed a methodology of looking for “robust theorems.”

Levins’ title was immediately arresting. Philosophers then didn’t talk about (heuristic) strategies, model-building or population biology. This was totally virgin territory. Model-building was a new topic for both biologists and philosophers. Both talked about theory—and treated their equations as completed edifices.<sup>1</sup> For philosophers, the only relevant contrast was between observation (or empirical evidence) that was given from nature and trusted, and theory—which was constructed by humans, and the best that we had, but still suspect. Theories were confirmed, disconfirmed, or yet to be tested. The context of justification gave the only subject matter then deemed appropriate for philosophers. Discovery or problem-solving was

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<sup>1</sup> The first textbook in this area that explicitly recognized that the equations presented were models and not established theories, and self-consciously discussed their shortcomings and idealizations, was Wilson and Bossert’s (1971) *A Primer of Population Biology*. An inexpensive paperback, designed as a supplement to “main” biology texts, it was also the first book published by Andy Sinauer’s new firm which targeted and became the premier publisher in this area.

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held to be idiosyncratic and unsystematic. Models (insofar as they were spoken of by philosophers at all) were interpreted as instances of theory—in a formal-logic driven account that gave us “the semantic conception of theories”—an idea that as far as I can tell has borne no fruit outside of philosophy. The ideas that there might be different kinds of theory or levels of theoretical activity, that theory was full of (non-deductive) heuristic approximations and articulations, and that model-building might be a structured and heuristic, but particularly tentative and exploratory activity with known false or oversimplified conceptual tools (Wimsatt 1987) were all beyond the pale. And that investigators tried to model phenomena (rather than theories) was thought to be conceptual incoherence (a view forcefully pushed by both Donald Davidson and Patrick Suppes).<sup>2</sup> From my experience at the time, topics connected with problem-solving and discovery were thought to be inappropriate or at best marginal for philosophers in any case.

But here were Lewontin, who had written a thought provoking paper on modeling in 1963 discussing his pioneering computer simulations of group selection (the t-allele in the house mouse, *Mus musculus*) and another particular 2-locus evolutionary problem (with fitness interactions between chromosome inversions in the Australian grasshopper, *Moraba scurra*) and Levins for whom theoretically informed (but more loosely connected) mathematical structures could be qualitatively analyzed without solving them—even if one had only partial information about the system (Levins 1974). For both of them, modeling was the cutting edge in the investigation of nature. They were the best in the business, and their work was fascinating. The philosophers had to be wrong.

Population biology was also a new subject—crafted by a number of innovative biologists—then young turks, but now almost legendary for the theoretical, empirical, and conceptual innovations they have spawned in the last 50 years. The group included Levins, Lewontin, Robert MacArthur, Ed Wilson, Egbert Leigh, and Leigh van Valen. The new perspective was crafted when they spent summers together in Vermont in the 1960s. They had concluded that ecology and the population genetics dominated evolutionary theory of the New Synthesis needed to be more closely articulated. These two fields, though in principle connected, had developed with at best weak links between them. There were no inter-level derivational or deductive relations to unify them. Community ecology had developed with conceptual tools derived for modeling the interactions of populations of diverse species who were born, lived, and died, (perhaps with multiple age-classes with age-specific birth and death rates), and who predated, parasitized, cooperated, and competed with one another in ways symbolized by one-dimensional lumped interaction coefficients. (Levins’ diagram of the structure of population biology was more complex—it contained 25 boxes of local models connected in a directed graph impinging on

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<sup>2</sup> I was surprised at the vehemence they showed in defending this belief. I remember describing scientific practice to Davidson, and saying that biologists must have meant something different by models than he did. His response was simply to say angrily: “Well, they’re wrong!” (end of conversation). Such hubris! This strange excursion from the real world is no-where better described and criticized than in Downes (1992).

community structure—the core model of ecology). To look just at how the simplifications in this area were related to population genetics, they didn't: in these models members of the same species were treated as genetically and behaviorally identical, and genetic variation was supposed to be irrelevant because any evolution was supposed to take place over much longer time spans.

Population genetics had correspondingly developed to emphasize only (a minimalist description of) the genetic structure of individuals, and simple models of who mated with whom. Fitnesses were add-ons to the models—generally postulated or measured in laboratory experiments and (very occasionally) in nature. But basically the phenotype was just treated as a black-box scalar multiplier for gene frequencies with (often arbitrarily assigned) selection coefficients. There were genes and chromosomes (or rather linkage coefficients) but nothing more complex than genes at 2 loci, and most theory and applications were pursued with single-locus models. Changes were assumed to take place over many generations, far longer than the seasonal fluctuations of ecological populations. There was no development and no physiology in such models, no ecology, no temporal variation of the environment, and a population structure not realistically hooked into the real spatial and temporal heterogeneity of the environment. So though basically of the same processes on different time scales, the relevant rates of change were held to be so different that they could be treated as decoupled. Both areas were grossly oversimplified.

The conviction that the articulation had to be made grew out of several things. Levins, MacArthur and Wilson were convinced that multiple components of fitness that keyed into diverse ecological and organizational conditions could show interesting tradeoffs (reflected most strongly in Levins' fitness set analysis and Wilson's ergonomics of castes and tasks in social insects) which they wanted to articulate with population genetic models. The theory of island biogeography of MacArthur and Wilson put more qualitative substance into local colonizations and extinctions in patchy environments that gave evolution an ecological time scale and population structures that also put Sewall Wright's population genetic theories involving small populations and a metapopulation structure into natural focus. And Leigh Van Valen, a polydisciplinary paleontologist urged a view of evolution as "the control of development by ecology" (Van Valen 1989). The gel electrophoresis applied by Hubby and Lewontin to sample protein (and thus genetic) variation in natural populations in *Drosophila* was rapidly diffused to other studies that showed seasonal variations of gene frequencies in voles, and spawned a whole range of studies in a similar vein. More recently, three generations of work by Rosemary and Peter Grant and their many talented students integrated ecology, seasonality, and mating history in multiple species of Galapagos finches and their vegetable and insect prey as measured in rich genetic, demographic and ecological detail, producing perhaps the most integrated studies in population biology to date—though much of this occurred well after the founding conceptual changes that brought the new hybrid discipline into being (Grant 1999).

This situation generated two important stimuli. First, phenomena in two fields were shown to be significantly coupled to each other. And second, mathematical ecology, demography (for age structure of populations) and population genetics,

then the three most mathematized fields in what were to become the Darwinian sciences, had a new need for comparability and articulation. But the complexity that had to be dealt with was potentially overwhelming. What to do? Many things, but the field was set for Levins' search for "robust theorems" that were true across multiple models that made different assumptions about a given phenomenon or relationship. In the face of incomplete data, with many practically unmeasurable key parameters, and the fear that many outcomes might be very sensitive to values of these variables or to as yet undetermined unrealistic descriptions in the models, the idea of an analytic comparison of models that might possibly span the range of possible states, relationships, and outcomes to look for robust results seemed both ingenious and attractive. But we needed to be at as much interested in models where the results broke down, since these showed the limits of robustness for the result. "Randomness and Perceived-Randomness in Evolutionary Biology" (Wimsatt 1980a) was in part a study of certain kinds of uncertainty (that Levins had used as an example of a "sufficient parameter" in search of a robust theorem) and also a study of and argument for the robustness of chaotic behavior in ecological systems.

I discussed Campbell's explicit writings developing what he called "triangulation" (e.g., Campbell 1966) more extensively in my 1981 paper on robustness, but the main distinguishing feature of his analysis was to emphasize the use of multiple perceptual methods to "triangulate" on the properties of objects not immediately known (things that were "distal"). He wrote far more on it than Levins, and had to deal with what was apparently a far more challenging context—namely the assessment of human characteristics using a variety of social science measures. For this he drew on analogies with perception—then a familiar area to psychologists. He also sought to argue for the "entitativity" of social collectives in terms of the agreement of multiple criteria for individuating them—or more generally on the reality of social factors that were insufficiently recognized by methodological individualists using the same criteria—multiple independent means of detection or measurement. His main challenge, I believe was the greater difficulty of distinguishing between parts of the detection instrument, or its effects and parts of the capability of object under study in the human sciences, although it is arguable that many artifacts in the natural science share exactly this feature. Indeed, I believe that this was just what characterized the "bacterial mesosome"—an artifact of preparation that was mistaken for a feature of cellular ultrastructure—discussed by Rasmussen (1993), Culp (1994, 1995), and Hudson (1999).

At the time I wrote the paper on robustness analysis for the Campbell festschrift, I tried to systematize the method, recognizing that robustness analysis proceeded from analysis of failures and limits of robustness as well as successes. I tried to draw together every methodological variation I could find that shared the use of multiple means of access, detection, inference or deduction to secure a more substantial handle on the phenomenon, object, process, or result under study, and found confirmations of it in some unexpected places. The resulting collection was very heterogeneous, but that was part of the point. All of these practices had some interesting things in common, despite their differences, and I wanted to mark these. But any comparative analysis must look to the differences as well as the similarities.

Others since (Weisberg 2006, Weisberg and Riesman 2008, Willinger and Doyle 2005, and Nickles, this volume) have noted the variety, and distinguished and elaborated some important sub-classes of robustness (Calcott 2010, and Raerinne 2010). I will make summary remarks on what are plausibly three main sub-types of robust inference, and then turn to a fuller commentary on the fourth, which is to look for and assess the significance of and use robustness in material systems.<sup>3</sup>

In my survey of eight kinds of applications in 1981, I specifically included three classes of cases:

- (1) Multiple means of empirical access or interaction with the target of investigation, in which I would include both different sensory modalities, and different instrument mediated paths to convergent or complementary result(s). This is in accord with our normal intuitions of regarding detection instruments as extensions of our sensory systems. Some of these amplify or magnify our existing senses to different size, time, or sensitivity scales, while others exploit different sensory modalities (e.g., magnetic anomaly detection) or sensory capabilities beyond the frequency range of our senses (e.g., UV or infra-red, or ultrasonic transmissions.) I had been thinking of radio-telescopic and light telescopic observation of the same objects, but I also included the possibility of theory-mediated analysis of the signal, such as an appropriately time-lagged correlation required to pick orbiting Phobos out of successive Mars images rather than have it averaged out as noise). The lovely study by Allamel-Raffin and Gangloff (Chapter 7) documenting robustness analysis with multi-spectral images using different instruments with different frequency filters and spatial resolutions elaborates the richness of this kind of analysis. Their analysis also involved a kind of calibration and also showed the use of theoretical knowledge of what kinds of emissions should covary in their robustness arguments. My original analysis argued for the importance of (the at least partial) independence of the detection channels, and this analysis was carried significantly further through the first-hand expertise of the talented and prematurely deceased Culp (1994, 1995).
- (2) A second important means is the use of different analytical methods. Here I included multiple derivational paths within a single multiply connected theory (Feynman 1967) and also multiple independently motivated and constructed models from which a common result could be derived (Levins 1966). Glymour (1980) clearly envisioned the possibility of the former kind of relationship

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<sup>3</sup> Brett Calcott (2010) has since produced a nice three-way classification in terms of multiple means between formal methods, detection, and material robustness (lumping the 1st and 3rd senses of the 4 discussed here). I agree with his classification: the distinction between my 1 and 3 can be seen as a distinction between kinds of detection methods, though it is also true that a model (from the “false model” perspective) can be seen as a kind of selective filter for the kind of pattern explored in the model. With that, only the kinds of exploration of the functions of multiple derivational pathways in a single formal system (like those investigated by Kromer here and by Corfield 2010) would stand out as a distinct kind. But to regard models as kinds of selective pattern detectors might violate too many intuitions!

though his network connections are ambiguous between analytic and empirical links. Ralf Krömer's (Chapter 8) work here breaks new ground in the richness of the functions he found for robustness analysis in mathematics, and how it made sense of existing mathematical practice and values. In this he has more than delivered on what for me were just at the time suspicions, and I look forward to more productive work in mathematics. An independent exploration of uses of robustness in category theory (developed in a somewhat different way) has recently been published by Corfield (2010).

- (3) Also empirically based, but quite different in character from physically or biologically based detectors are those that make intensive use of intentional responses, such as questionnaires and various kinds of more passive survey data. Derived from these are the kind of multi-dimensional index construction utilized in the social sciences, and still nowhere better expounded than in Campbell and Fiske's classic 1959 paper: "Convergent and Discriminant Validation via the Multi-trait Multi-method Matrix". This mode has not been discussed here, but it also appears to be more treacherous ground.<sup>4</sup> (But see Trout 1998, who urges and uses robust methodologies in the human intentional sciences).

Each of the first two of the above categories have seen expansive and creative discussion substantially increasing both the reach and qualifications on the use of robustness concepts both in this volume and in the intervening years in the literature, mostly initiated by rediscoveries of Levins' work by Odenbaugh (e.g., 2006) and Weisberg (2006)<sup>5</sup>.

In that survey I did not consider some of the social structures and interactions that give robustness, from multiple eyewitness testimony to the structure of juries although I have explored some of them in teaching. Reproducibility in different labs (which are never exactly the same conditions (Waters 2008)) and with different preparations secures some robustness, as (ideally) does peer review—though the

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<sup>4</sup> Twenty years after Campbell and Fiske (1959), that paper was the most cited in the journal, which asked Fiske to review the 2000+ citations it had received to assess the role the methodology might have had in generating progress. Most citations were obligatory "field" reviews that cited but made no use of it, and the success from the much smaller number that did discuss or use it was very disappointing. (The original was in the domain of personality theory, which has been a minefield for attempts at "objective" or "valid" classification scales, so perhaps it would have been better in other areas.) I wondered whether a particularly severe problem in the studies reviewed was in separating the phenomenon being investigated from the tools of analysis, and Fiske agreed (in conversation, 1982). We usually have clearer conceptions where one leaves off and the other begins in the biological and natural sciences, but when this fails, it should be problematic for any robustness analyses.

<sup>5</sup> In Wimsatt (1991), I discuss how multiple views (in this case, 4 different graphical representations of a chaotic phenomenon) were required to understand it. These views are not independent (they are analytically related), but the different representations are crucial to being able to see different aspects of the phenomenon. This is a kind of visual robustness, made relevant by the limitations of our visual and cognitive apparatus.

latter may more often serve to indicate things that should be done to check or to investigate robustness than confirm it. Similar things are represented in the decision to assemble investigators with diverse experience in a single lab to work on a class of problems, and different styles of investigation in different disciplines or different national styles in different countries may lead to investigation of a phenomenon under different conditions that we need to understand the larger picture. Thus it is probably no accident that the character of the *lac*-operon which gave us the first insight as to the mechanisms of gene control and gene expression, would have been disentangled in France, where there was much more emphasis on the physiological dimensions of genetics than in the structurally dominated traditions in England and biochemical hegemony in the U.S. (Burian and Gayon 1991; Morange 1998).

I also considered “pseudo-robustness”—cases where the presumed independence of means necessary for robustness was compromised in ways that were not obvious to the investigators, and where later investigations could show that the arguments for robustness were unsound. The most striking case of this I discussed at length in 1980b—the fallacious arguments against group selection, where the ineffectiveness of group selection appeared to be a robust result across 12 mathematical models. These were shown by Wade (1978) to depend upon 5 false simplifying assumptions. I argued then that the culprit was a common set of heuristics in reductionistic model building, and proposed a systematic corrective in the form of inter-level cross checking of assumptions. (Thus things that looked plausible at a lower level that made simplifying assumptions about the environment could be more easily seen to be unrealistic when one went up one level and considered what were the major relevant organizational features of the environment. And of course, for symmetry, one had better check at lower levels to see that the properties supposed in the model at a given level are indeed robust under the conditions supposed). It seemed to me then, and does so even more now, that demonstrating independence, or characterizing its range and limitations (which also indicates the range of robustness claims), and analyzing any systematic biases in the perspective of existing models, however caused, is a crucial and difficult activity, and indicates again that robustness is no silver bullet. Also left out of my characterization at the time was any attempt to characterize the strength of robustness claims in ways that indicates that different links or paths might have different force or bearing on the central claim said to be robust. This has since been pursued by others—e.g., Stegenga (2009), and by Soler in her introduction to this volume.

### 3.2 Material Robustness

The methods discussed so far can all be characterized as “inferential robustness.” They do not primarily touch on the robustness of phenomena or behavior of objects, except peripherally. In that original sweep of the family of methods relating to robustness, I reached as far as multi-level mapping between states (such as one

might find between micro-states and macro-states in statistical mechanics, or molecular and classical characterizations of the gene),<sup>6</sup> and the processes involved in looking at matches and mismatches between descriptions for things that needed to be changed to improve the fit and to develop interlevel explanatory accounts. Rich connectivity has played a crucial role in the development of inter-level mechanistic explanations in genetics and elsewhere (Culp 1994, 1995; Wimsatt 1992).

Robustness and reliability have been deep and entrenched biological design principles in nature throughout evolutionary history. It is not surprising that we should naturally use multi-modal calibration, checking, and inference as an adaptation. Not only does it improve the reliability of our inference and action in the world, but the world itself would not be one in which complex organization could have evolved but for a rich fabric of robust and stable interactions on different size and time scales. This was a central focus of my analysis of levels of organization in 1976, 1994, and 2007b. The analysis of levels of organization using robustness is particularly interesting for philosophy because it would appear that with it, one is getting interesting ontological claims out of broader empirically grounded relationships. Philosophers have of late tended to deny bases of metaphysical claims in empirical relations, no matter how general.

In attempting to analyze what a level of organization was, I moved away from the then universal tendency to discuss such topics as reduction as a relation between theories, which came in levels, and argued that we needed to understand reductive explanations in terms of relationships between phenomena, objects, and regularities at different levels of organization (themselves characterized in terms of robustness). Theories came in levels because levels in nature were the loci of multiple regularities and stabilities among objects and relationships, and one could get a “bigger bang for a buck” by building theories about the entities and relationships one found there (Wimsatt 1976, 1994, 2007a). This would lead naturally to an investigation of material robustness of properties and phenomena in systems, rather than to robustness in our inferential means of determining their properties. This (and the natural robustness of objects in our world) could have been seen as primarily to indicate why it was adaptive that we use robust inference. The discussion in the 1981a paper focused primarily on robust inference rather than robustness in material objects, although my earlier discussion in 1980a considered an important case study, the robustness of chaotic dynamics in ecological systems.

In the intervening years, attention has turned much more intensively to investigations of robustness of natural objects, or of behaviors or properties of natural objects. This has turned out to be particularly useful, as Tom Nickles’ (Chapter 14) work has indicated, in the analysis of networks, which might to a prior generation have been seen as rather problematic objects. (Thus Campbell went to great pains to argue that social groups could be seen as entities in terms of the robustness of their

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<sup>6</sup> The relation between molecular and classical conceptions of the genes is heterogeneous on both sides, and much more complex than between micro-state and macro-state descriptions in classical mechanics—roughly because there are many mechanisms between micro- and macro- in genetics and many more kinds of anomalies possible (see, e.g., Beurton et al. 2000).



boundaries—generated in terms of their properties as a social network.) With the development of theory, by Watts and Strogatz, Barabasi, and others, for describing the connectivity properties of networks and their consequences, it has emerged in these analyses that some properties of these networks are both interesting and robust. This work in turn can be seen as a conceptual development in a lineage pioneered earlier by Rosenblatt (1958) in ensembles of idealized neural networks (his “perceptrons”) and the later development of connectionist networks in the mid-1980s. Both looked for properties common throughout the ensemble of networks meeting certain conditions, and the work beginning in 1969 by Stuart Kauffman looking for self-organizing or generic properties of gene-control networks (things like mean length of cycles as a function of number of nodes and connection density) has this same feature.

### 3.3 A Central Biological Example: How Is Sex Possible?

A major driver of this interest has been to understand the architectural features characterizing biological organisms that allowed them to be so tolerant of and able to maintain behaviors or states or their characteristic features across generations in the face of environmental or genetic perturbations. I describe here what I take to be the most interesting (and indeed most focal) problem involving robustness in biological organisms. I have taught this case for nearly 30 years as a general puzzle for the architecture of genotype-phenotype mapping that needed solution (Wimsatt 1987, 2007b, Chapter 10), and was long surprised that it was not discussed. This has changed—it is now recognized as important, and I regard it as at least partially solved by the discussions of Wagner (2005). This is what I would call “the paradox of sex”, or

“How is sex possible?”

The developing organism is systematically tuned (as a matter of design) so that small differences can have effects on a variety of size scales including the very large, in which context dependence of effects is a common phenomenon, but where it is crucial that most differences do not have significant effects most of the time. Thus the organism can be very responsive to small genetic differences or differences in environmental stimuli or resources, but it is crucial that these not disturb crucial remarkably stable and regulatory species specific developmental and behavioral patterns. (Those used to inter-level relations of the sort characteristic of classical statistical mechanics, where “law of large number” averaging is a reasonable mode of moving from one level to the next, will find the complex interplay of sensitivities and regularizing equilibrations of the relations between genotype and phenotype to be quite remarkable.)

This is a kind of “sloppy gappy” robustness, which can be full of exceptions and where what is required is just that the desired result occur sufficiently frequently—the normal state of affairs in evolutionary contexts. This is because selection works

on performance that is only sufficiently regular. Because of the complexity and context dependence of the desired states, crisp regularities are unattainable, but also unnecessary.

Consider the following:

- (1) We are given the genetic variability at many loci (of the order of 5%) characteristic of virtually all species of organisms. With a genome size of 25,000 genes, this would mean that 1250 genes are segregating. With just 2 alleles per locus, (since  $2^{10} \sim 10^3$ ) this yields on the order of  $10^{375}$  possible genotypes, and this is an underestimate, since there are often more than 2 alleles per segregating locus.
- (2) We also have the scrambling effects of genetic recombination, so that each offspring is essentially without precedent in the specification of its genotype. Offspring of the same parents (save for identical twins) should characteristically differ at many hundreds of loci or more.
- (3) Furthermore, we know that small genetic changes can and often do have large effects, and that interaction between genes in producing their effects is the rule rather than the exception. Indeed, characterized biochemically, almost all interactions are epistatic or non-linear in their effects.

Given these three facts, it is remarkable that any regularity in heredity ensues at all. It would be plausible to expect almost no correlation in phenotypic properties between different members of a species (within the range of properties defined by that species), or between parents and their offspring, and especially to expect frequent lethal interactions. But this would render evolution impossible.

- (4) Yet offspring commonly inherit their parents' traits, as well as their fitnesses—not perfectly, but much better than random. The frequency of spontaneous abortions among women of peak reproductive age (25–30 years old) has widely divergent estimates but appears to be somewhere between 15 and 60% (with the higher estimate arising from sub-clinical abortion events undetected by the mother).<sup>7</sup> Many of these involve chromosomal anomalies, with predictably severe results for missing or added chromosomes. But just given the normal genetic variability, even without chromosomal abnormalities, how come mortality is not 99% or more for a normal genomic complement of alleles that have never appeared together? How come all of the nonlinear interactions don't just produce gobbledegook?

For evolution to be possible, there must be heritability of fitness, and to adapt successfully in different environments, it must be possible to select for diverse sets of characters giving adaptation to those diverse environments. This requires not only the heritability of fitness but the heritability of characters or character arrays. Both require the general stability of the species-specific phenotype at many

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<sup>7</sup> There are surprisingly few papers estimating this, and fewer recently. Roughly 15% of eggs fail to implant. Estimates of the frequency of first trimester abortions varies substantially between 15 and 30%. Boue et al. (1975) is the most common citation.

levels. Not only must elephants breed elephants, humans humans, and *Drosophila Drosophila*, but the variability and systematic and independent inheritance of individual survival-relevant characters from parents to offspring within each species must be preserved—not glued together with a thicket of epistatic and linkage interactions, or commonly shattered when they are broken up—if temporally and spatially local adaptation to changing environments is going to be possible. We are constantly told of cases where a single base change in a gene or a single amino acid change in a protein has enormous consequences for adaptation and function at a variety of higher levels of organization. But this must be the exception rather than the rule for evolution as we know it to be possible. (Sickle-cell anemia remains the classic case here, and there still aren't many cases known as yet, though these should increase with our knowledge of developmental genetics.) Nonetheless, the plain fact remains that most genetic changes that happen under biologically normal conditions have no readily discernible effects. (See Lewontin 1978 on “quasi-independence”—the ability to select for one character in evolution without transforming or dragging along a number of other characters, and Wimsatt 1981b for further discussion.)

Wagner (2005) surveys robustness in biological organization in multiple adaptive systems at multiple levels, from the mappings in the genetic code (both the redundancies, and the non-random higher frequency of 3rd position mutations to another amino acid that preserves hydrophilic or hydrophobic interactions at that position) up through various cellular and developmental processes showing multiple pathways and canalizations. I believe that these multiple piecemeal robustnesses and canalizations go a long way to explaining a deep puzzle: the possibility of the heritability of characters and fitness in sexual species with normal degrees of genetic variability. Since there is significant genetic variability in natural populations, a great deal of epistatic (non-linear) interaction between them, and sexual recombination produces genetic combinations that have never arisen before, the heritability of characteristics is a mystery. But given the surveys of robustness discussed by Wagner, in effect, we are exaptively prepared for sexual recombination with the causes of robustness arrayed in a diffuse and distributed manner.

But these may just as well be an effect as a cause, or over time, co-causal with resultant population genetic dynamics. Livnat et al. (2008) urge that under some conditions, in sexual species, the ability of an allele to perform well across diverse genetic backgrounds will be selected for, and model this alternative arrangement. They conclude that selection for this would be especially strong in transient conditions—i.e., those with mixing of populations having a diversity of alleles some of which do not mix well. So it would seem that starting with enough exaptive robustness for sex to be viable (as noted by Wagner), this process should drive evolution to a state in which there is widespread heritability of fitness of alleles across backgrounds.<sup>8</sup> Livnat et al. also note that this process would increase additive

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<sup>8</sup> This raises questions about Wagner's assumption that environmental fluctuations should be a stronger driver than genetic compatibilities. As I noted in (2006) he considered only mutation and ignored recombination, which could produce variances that would be orders of magnitude higher than those produced by mutation—though of course not necessarily larger than environmental variance.

components of fitness in such alleles, a possibility I raised in 1981b, p. 146, as a product of selection for the arguably equivalent “quasi-independence” of characters noted as a requirement for evolution by Lewontin (1978).

There are interesting possible parallels here with the evolution of standardization for machine parts, or cross-platform compatibility of software in the evolution of technology, or training for professionals that require certain competencies. In all three cases, things that transport better to other contexts should be selected for, and this applies not only to things like absolute compatibility but to convergent pressures to adopt a common interface, where the cost here is in the steepness of the learning curve for divergent applications.

To return to the biological case, we have robustness apparently increasing evolvability. Wagner addresses the apparent conflict here: shouldn't robustness decrease pressures and potential for evolution by increasing stability of the phenotype and not showing alternative states to selection? His answer is to argue that if robustness, by allowing the accumulation of greater redundant complexity, also generates a larger state space, with more variability that may be expressed under different conditions, then robustness increases the possibility of normally unexpressed variability that may emerge under new conditions. This plausibly involves an increase in evolvability. In so doing he is supposing that robustness—despite first appearances—is context sensitive, urging something that Nickles has emphasized in his contribution for this volume.

### 3.4 Qualifications on Robustness

Tom Nickles' suggestion that robustness should actually be regarded as a 4 place predicate: “system  $S$  is robust to perturbation  $p$  in degree  $d$  except where  $c$ ” seems exactly right. These or some such similar qualifications seem appropriate. Any piece of detection machinery can obviously break down in ways that are suggested by its architecture, and any tool must be used in a way appropriate to its organization. And any specific kind of linkage will be sensitive to some kinds of stimuli and perturbations and insensitive to others, and usually, to various degrees. Material robustness calls for a study of these qualifications. I argued above for a kind of statistical robustness in adaptive organization which is “sloppy gappy” driven by the characteristics of selection processes. But there are others.

There are some potential ambiguities in the arguments Tom has accepted (from Doyle et al. 2005) that selection for increases in robustness will tend to increase complexity, and that in turn will increase fragility. He has referred to a common occurrence in the evolution of technology. But here we need to distinguish between potential fragility and actual or probable failure. While it is true that adding new linkages or mechanisms to a system to increase robustness can also introduce new failure modes, this does not mean that probability of failure would be increased over the range of conditions where such a system is normally used. The characterization I gave of robustness was purely topological—it pointed to the ways in which alternative parallel paths would increase reliability if there were no changes in the

reliability of component linkages, either due to their architectural redesign or to base reliabilities in the components. Changes in these may increase or decrease overall reliability.

Anyone driving a car 50 years ago could expect far more failures than they would now, even though with the increased complexity of a car's operating control systems and their dependence on micro-processors, we have given up even the ability to identify necessary repairs, much less make them, although to someone having the appropriate computer diagnostic tools that utilize all of the imbedded sensors in the cars' control systems, the chances of correct diagnosis may be significantly increased. Obviously there are now many more ways in which such a system can fail, but the net reliability and usability of a computer-controlled injection and ignition system (improving cold weather starting and eliminating hot weather vapor-lock) is apparent to anyone who has to start a car on a cold morning. Note that here we have increased the robust operating range of the engine—something often found with continual design refinements. Finer machine tolerances have decreased oil consumption, while computer controlled ignition and valve timing, and the introduction of 4 valves per cylinder have increased combustion efficiency and reduced fuel consumption while increasing specific power output. Synthetic oils have increased the time between oil changes and the mean lifetime of engines has increased. While it is true that the use of electronic components means that they can fail in several new ways (they could be burned out by the electromagnetic discharges induced by a nuclear explosion,<sup>9</sup> there are new possibilities for programming errors (apparently the cause of anomalous acceleration found in 2008 in a variety of Toyota automobiles) or hardware wiring errors. Indeed, the increasingly smaller size of integrated circuits generates an increasing chance of cosmic-ray induced errors. For all of this, the net effect has been significant increases in the reliability, tractability, and efficiency of running engines.

And this reticulate complexity also infects inferential robustness in complex experimental and detection systems. All of this is suggestive of the reticulate complexity of nested analytical and control procedures documented by Lena Soler (Chapter 10) in her rich and beautifully detailed discussion of analytical and experimental robustness in the demonstration of weak neutral currents. But the very complexity allows inferences that would not have otherwise been possible. So is this increased fallibility, or robustness over a greater performance range? Probably both.

What has happened with the technology of automotive engines is that the engines in question have evolved so that they would now be characterized by a state-space with more dimensions. If at a molar level, they still have the same number of functional systems however, we can say that there is a mapping from the later larger

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<sup>9</sup> When I worked at the National Cash Register Company (NCR) in 1962 designing adding machine components, there was a sudden interest in hydraulic logic computers, which mimicked electron flows with water streams, exhibited by the defense department. These would be isomorphic to electronic ones (with diodes, adders, and registers), but would not be sensitive to electromagnetic fields induced by nuclear weapons. Their multiple other disadvantages ruled them out however.

number of variables of the newer state space into the smaller number of variables characterizing the functional organization in the older one. And the net lumped failure probabilities in the older (or lower resolution) state space may have decreased even though there are now more ways to fail. So while increases in complexity may generate new kinds of failure modes in systems, this is quite consistent with net increases in overall system robustness. In addition, of course, if we learn more about the system and how its links interact with each other and with inputs to the system, we may better understand its proper calibration and limitations of its use. How much of this also affects the instrumentation and experimental checks of the apparatus for detecting weak neutral currents?

### 3.5 Robustness and Entrenchment

Finally, robustness, canalization, or other forms of stabilization in biological organization, whether genetic or environmental, and however secured, should provide a primary target for generative entrenchment. Generative entrenchment of an element is a state in which the action or presence of that element has many and diverse consequences for the further development of the phenotype or system in which it is embedded. Things that are deeply entrenched are things that are very conservative in evolution because their change or disruption has a high probability of having far reaching negative fitness consequences. In an evolutionary process, changes are made that act in ways that are modified by the existing dynamical structures in the system. For heritability of effect, mutations would be favored that plug into elements of the developing system that are stable—i.e., robust elements or behaviors, and other things build on these. As a result increasing chains of dependencies are constructed that act in ontogeny, and the more deeply entrenched elements acquire a longer history. Also as a result entrenchment (as “pleiotropy”) becomes a powerful tool to analyze developmental architectures, and is widely used to construct phylogenies. So robustness acquires indirectly yet another critical role in the analysis of biological systems. But this is another story (Wimsatt 2001, 2007b, Chapter 7).

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