Conclusions

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What can we conclude from this set of chapter about limits to knowledge in evolutionary genetics? The very question requires that we look into the future and imagine those areas that will be forever refrac-tory to future innovation. This is a daunting task, because we are participants in an era of unparalleled technical innovation in biology. We have seen biology answer questions that seemed beyond the bounds of knowledge a decade or two decades ago. We are confident that the future will replicate the recent past and produce answers to today's seemingly intractable problems. Many of the chapters in this volume reflect this view and reflect the problem of separating the merely difficult from the set of biologically interesting questions that lie beyond the bounds of knowledge.

There are two big questions in biology: How does the organism work and how did it get to be the way it is? The first question is the province of cell, developmental, and physiological biology (and all their specialized descendants), but it is also fundamental to understanding biological adaptation. The second question is the major concern of evolutionary biology. (I include the problem of prediction within this second category.) I think it is fair to say that the larger community of biologists is confident that we will understand how the organism works in exquisite detail. To illustrate how our grasp of this question has changed, I recall as an undergraduate student more than 35 years ago taking introductory biology and finding that the text included a section entitled "what is life." This section included a serious discussion of *elan vital* and the notion that understanding life might involve extraphysical explanations. It is difficult to imagine such a discussion today. We are absolutely committed to the notion that physically based and mechanistic explanations of how the organism works will be obtained. Certainly the recent progress of biology provides a strong basis for such confidence.

The second question of how did life get to its present state is more

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problematic (as is the corollary of how do we use our understanding in the prediction and management of biological systems). Our understanding of the past is rooted in the theory of evolution by natural selection. This is a statistical theory, but as noted in different ways by several authors, we have just one realization of the stochastic process of earthbound biological evolution to study, and it is not very informative to apply statistical means to the understanding of a single realization. It seems clear that our understanding of the past and our ability to predict the future will remain hazy and weakly defined. That is not to say that we cannot understand the broad outlines of biological history, but rather that we are unlikely to know the precise historical scenario.

Because of the statistical nature of genetic transmission and natural selection, our theories of the past and future are broad generalizations that do not provide a detailed explanation for the particular outcomes that we study as biologists. A place where this theme of the particular is especially apparent concerns the issue of biological interaction. Biological organisms clearly exhibit strong interactions at the molecular, developmental, and metabolic levels, so there is good reason to believe that interaction also is manifest at the statistical level, but our theoretical tools for studying biological systems are based on the minimization of interaction in the interests of generality and tractability. Several authors discuss the problem of biological interaction in different contexts. Because the biological system is complex, with thousands of actually or potentially interacting components across both the genetic and environmental dimensions, the ability to understand and predict the statistical behavior of these systems is limited.

Let me conclude with one final thought. The triumph of the physical sciences was to deduce a set of laws that govern the behavior of physical systems. This law-bound framework defines the possible. Rosenberg (Chapter 3) argued that evolution, and hence, all of biology, is governed by the law of natural selection and that this is the only law in biology. Despite the fact that the theory of evolution by natural selection is the major unifying law of biology, over the past 25 years, evolutionary genetics has focused a great deal of attention on nonselective causes for molecular evolution. This focus on neutrality has been of value because it has presented a clear and well-defined null hypothesis for statistical analysis, but it also has directed attention away from the central problem of biological adaptation. What a curious detour to have so much attention to be devoted to nonadaptive explanations for molecular diversity. Perhaps this detour reflected the social environment of the times. The notion of subjectivity in science appeared in several chapters in terms of Baysean priors or in terms of our collective judgment on what constitutes an interesting question. A limit to knowledge may simply be our belief systems and their role in determining the directions that our search for knowledge takes.

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