selection, selective ratchets, ontogenetic ratchets, species selection, and recapitulation. Even the concept of viviparity gets a working over.

A decade ago S. J. Gould and R. C. Lewontin published their now famous paper "The spandrels of San Marcos and the Panglossian paradigm: A critique of the adaptationist programme" (*Proc. R. Soc. London B* **205**, 581 [1979]). There they assaulted sociobiology by attacking an often naive presumption of those who speculate about adaptive significance, namely that all conspicuous features of living organisms are necessarily the perfected products of natural selection. Gould and Lewontin were going at the philosophical roots of sociobiology but in so doing put many evolutionary biologists, particularly morphologists, on the defensive. To morphologists trying to understand adaptation in the vernacular sense, the scoundrels of San Marcos had gone on an anti-adaptationist pogrom. The word "adaptation" has been shunned during the past decade by many, including some contributors to this volume.

As an evolutionary biologist interested in vertebrate design, I was pleased to see in this book that adaptationists' speculation has survived the 1980s. This book is full of rich scenarios for the evolution of complex organismal functions (=adaptations), even if the word "adaptation" didn't quite make it into the title. If there is a single dictum subscribed to by all the contributors, it is that one *can* legitimately speculate about adaptations and their evolutionary significance, *but* to be credible such speculation must be done within a tight phylogenetic framework, where the phylogeny is richly supported by characters other than those under study.

In the final analysis, though, Dahlem workshop reports don't work very well as books, even when compared with those generally unreadable entities, conference proceedings, that invade our library shelves. The breadth of ideas presented—a predictable result of the nature of the workshop—means that a reader must be exceptionally knowledgeable to follow all topics covered. It also means that some first-class review articles included in the reports may be hidden from their mainstream fields. Two examples from this book are the chapters by the embryologist R. P. Elinson on egg evolution and the neurobiologist G. Székeley on the neuronal structures controlling tetrapod locomotion. But there are many more.

Few people are likely to read this book in its entirety. Yet there are enough interesting papers in it to make it worth flipping through for any vertebrate biologist with a passing interest in evolution, even if not caught up in the issue of "integration of complex organismal functions."

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Low Probabilities

Large Deviations. JEAN-DOMINIQUE DEUSCHEL and DANIEL W. STROOCK. Academic Press, San Diego, CA, 1989. xiv, 307 pp. $34.95. Pure and Applied Mathematics, vol. 137.

The theory of large deviations comprises the art of estimating with some precision the probabilities of certain rare events. In such estimates there is usually a parameter having some physical significance and the model, the event, or sometimes both depend on this parameter. As the parameter gets large the event in question becomes less and less probable, and one is interested in knowing as precisely as possible the exact rate at which its probability goes to zero.

Such problems arise in different contexts. For example, an insurance company might want to know the probability of a certain catastrophic loss. The Scandinavian school developed the large-deviation method in the 1930s for this purpose. Sometimes one may have to compare two rare events and determine which is likely to occur first if one waits long enough. There are several concepts in statistical mechanics that can be interpreted in terms of large deviations of one type or another.

What makes the theory of large deviations particularly attractive is that the probability of the event of interest is often exponentially small in the natural parameter with an exponential constant that can be exactly evaluated. Moreover, this constant has an appealing physical interpretation involving entropy of some sort. This close physical connection has made the subject particularly attractive to mathematicians and physicists in recent years.

The present book by Deuschel and Stroock investigates several natural contexts in which large deviations arise. Though there is no universal theory that encompasses all these situations, there are some general principles or themes that keep coming up. Convex analysis, Laplace asymptotic formulas, and relative entropy are some of these. The early chapters of the book are devoted to some of the standard examples: Cramer's theory for sums of independent random variables and Sanov's theory on the large deviations of the empirical distribution. The first example is the more elementary, but one can see the relative entropy come up naturally in the second. The large deviations of Wiener measure and the related theory of Ventcel and Freidlin on small random perturbations of dynamical systems are a remarkable example of the success of the theory. These are also dealt with carefully in the early chapters of the book.

The later chapters deal with large deviations of the occupation measures of Markov chains and processes. This theory was developed by Donsker and Varadhan and independently to a lesser extent by Gartner. Here ergodic properties of a Markov process play an important role and logarithmic Sobolev inequality and hypermixing are crucial analytical tools.

The interested reader might profit by going through additional material, especially with regard to connections with equilibrium statistical mechanics. References 39, 73, and 93 are possible sources for this material.

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Protein Structures

Prediction of Protein Structure and the Principles of Protein Conformation. GERALD D. FASMAN, Ed. Plenum, New York, 1989. xiv, 798 pp., illus. $95.

The ultimate solution to the "protein folding problem" will be the elucidation of the "second genetic code" relating the amino acid sequence of a protein to its secondary, tertiary, and quaternary structures. Although there is as yet no indication that a general solution is forthcoming, considerable progress has been made, and this volume of 20 chapters by some of those most active in the field is meant to bring it to the attention of a wider audience, at the same time making available many of the computer programs that have been developed.

Many different aspects of the subject are presented here. When the "energy" minimization approach (discussed here by Mackay *et al.*) was found to be impractical, attention shifted to using known structures to elucidate empirical rules of protein structure. Initial efforts attempted to predict simply the segments of secondary structure (α-helices, β-strands, and reverse turns), on the assumption that these regular local structures were determined primarily by the intrinsic tendencies of the individual residues, plus interactions with neighboring residues in the sequence. The results were initially impressive but failed to improve substantially; generally, about 60% of residues can be

classed correctly as helix, strand, turn, or irregular. It now seems clear that the secondary structure is determined to a significant degree by interactions in the three-dimensional structure between residues distant in the primary structure. The most striking demonstration of this is that 80% of pentapeptides with the same sequences have different conformations in unrelated proteins (although the relevance of this observation is disputed by the editor on p. 220). The more adventurous now attempt to incorporate tertiary structure into their predictions by using concepts such as amphipathicity (discussed here by Finer-Moore *et al.*) and hydrophobic moments (Rose and Dworkin; Eisenberg *et al.*) and distinguishing between different classes of tertiary structure.

Most attempts to predict protein tertiary structure concentrate upon finding patterns in sequences that are compatible with a single conformation that is already known, and there have been some noteworthy successes of this approach. In 1979, Ptitsyn, Finkelstein, and Murzin predicted the unknown protein uteroglobin to have four α-helices and proposed that it had a four-helix bundle structure, like that found in several known proteins. When the crystal structure was subsequently determined, the four helices were confirmed, but the dimeric molecule had them packed together somewhat differently. This structure also contained two unnatural disulfide bonds, however, and the natural protein demonstrates considerable flexibility, so the verdict on this prediction needs to be reserved. More recently, in 1987, Crawford, Miermann, and Kirschner analyzed the sequences of ten tryptophan synthase α-subunits and noticed that eight repeated β-strand/turn/α-helix/turn motifs were predicted. This suggested that the tertiary structure is an eightfold α/β barrel of the type observed first in triosephosphate isomerase and subsequently in at least 15 additional proteins with apparently unrelated sequences. The crystal structure of the α-subunit entirely confirmed this prediction. Interestingly, another prediction was misguided by experimental evidence that the protein contained two independent domains. In the same year, Pearl and Taylor were able to match the sequence of an HIV protease with the acid protease structure and to propose a model for the HIV protease that was largely confirmed. Regan and DeGrado reported the successful preparation of a four-helix protein that had been designed entirely de novo. Although the exact structure has not yet been determined experimentally, all the evidence is consistent with its being the intended conformation. The folded conformation is remarkably stable, which is perhaps the most impressive demonstration of the advances that have been made. Unfortunately, none of these accomplishments are mentioned in this volume.

Other shortcomings of the volume are common to multiauthor works: the unevenness of presentation (one chapter, Fasman's account of the development of the subject, is 124 pages long, whereas six are no more than 16 pages), that half of the chapters were apparently completed three years before publication, others one year, and that some authors fail to address the topic of the volume, concentrating instead on their usual interests. For readers in quest of the Holy Grail of protein prediction, however, this will hardly be noticed, for they will be engrossed in the large amount of detailed information available.

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