

Book Reviews

Baboon Metaphysics: The Evolution of a Social Mind.

By Dorothy Cheney and Robert Seyfarth. x + 347 pp. Chicago: The University of Chicago Press. 2007. \$27.50 (cloth).

In a primatological *tour de force* surpassing even their previous classic, *How Monkeys See the World* (1992, University of Chicago Press), Dorothy Cheney and Robert Seyfarth summarize 15 years of research on the social relationships, cognition, and communication of the baboons of the Okavango Delta. The book begins with Darwin (“He who understands baboon would do more towards metaphysics than Locke”—Notebook M, 1838) and a brief history of scientific thinking regarding the operations of primate minds, from Aristotle to the present. Next, the authors explore views of cercopithecine minds specifically, by pulling accounts of monkey behavior from European, Japanese, and ancient Egyptian texts, and adding more recent accounts by Africans. The authors document baboons’ cognitive feats under unusual situations, when local people have employed them as goat-herders (who require no training to flawlessly match large numbers of lambs with their mothers), mechanic’s assistants, oxcart drivers, or railway signalmen.

Chapters 3–5 introduce the reader to the sorts of challenges that baboons must solve in the wild—predator attacks, deep water crossings to get from one island to another in the flooded delta, infanticidal immigrant males, dominance struggles, and the complexities of daily social life, in which each individual is competing with many rivals for access to food and preferred social partners. A notable strength of this research program is the inclusion of hormonal analysis. By extracting hormones from fecal samples, their research team was able to measure changes in glucocorticoid levels as a function of the types of situations the baboons encountered. This meant that the researchers could know exactly how stressful particular types of events were for the animals, rather than relying on intuition. Presumably, natural selection has shaped baboons’ minds such that they have stronger stress responses to those situations that have had the biggest impact on their fitness over the course of evolution. One of the biggest strengths of Seyfarth and Cheney’s cognitive work is the fact that it is grounded in a detailed knowledge of the animals’ natural history. Their experiments are performed in the field, and they ask the animals to solve those same types of problems that they face in daily life, solving the sorts of challenges that they have presumably been confronted by throughout their evolutionary history. For this reason, they surpass all other scholars in their ability to design experiments that have relevance to explaining the evolution of mind.

In the latter half of the book, the authors delve into the main subject of their book. They start by documenting how baboons, like vervets, have an intricate knowledge of the rank, kinship, and alliance structure of their group. The authors postulate that in order to keep track of so many dyadic and triadic relationships (82,000 triads in a typical baboon group), the monkeys must be developing theories of social life—general expectations about how social interactions are likely to unfold (e.g. expectations about rank transitivity, tendencies for kin to support one another, and expectations about how males and females will behave in

consortships) rather than relying strictly on associative learning. In other words, baboons have an innate predisposition to recognize certain features of others’ social relationships. This knowledge has a hierarchical structure. Furthermore, baboons have an elementary theory of mind. That is, they seem capable of intuiting the motives and intentions of others (e.g. willingness to defend access to a resource), even though they seem not to attribute particular specific sorts of knowledge (or ignorance) to them. The authors show, via a series of ingenious experiments, how particular vocal signals are interpreted differently by the animals, depending on who is producing them and what recent social interactions might have affected the motives of the vocalizers. Thus, mental representations of individuals, their intentions, and qualities of their dyadic and triadic relationships, are combined in ways that are somewhat analogous to human language. The authors propose that nonhuman primates’ abilities to manipulate these mental representations in a discrete combinatorial fashion and to encode propositional information are a sort of “language of thought” that preceded and was a preadaptation for human language. They retain their earlier opinion that nonhuman primate vocal communication lacks many of the features of human language (e.g. nonhuman primates are remarkably inflexible when it comes to call production, though they are more plastic regarding vocal comprehension and usage). But they argue that in the quest to explain the evolution of language, too much emphasis has been placed on call production and too little emphasis on the cognitive aspects of language.

This book is necessary reading for anyone interested in the evolution of language or intelligence. The writing is accessible enough that any layperson interested in evolution or animal behavior would find it engaging, and yet it has enough new ideas and empirical facts to fascinate professional primatologists as well. It would be an ideal supplementary text for undergraduates studying primate behavior or cognition. This book includes highly cogent summaries of the theoretical issues relevant to the evolution of intelligence and language, complete with references to guide readers to additional reading. It also provides extensive detail on methodologies used for teasing apart the workings of the primate mind in the field. Cheney, Seyfarth and their colleagues approach cognitive issues from many angles, incorporating playback experiments, hormonal analysis, and standard ethological methods, to produce a highly convincing model of how baboons perceive and manipulate their social environments. Surely even the most learning-resistant student could hardly fail to be charmed by the cleverness of the experiments, the humorous fieldwork anecdotes, and of course, the daily drama of baboon life. Descriptions of the research are peppered with enthralling nuggets of natural history that have never been published elsewhere, 45 superb photos, and amusing literary allusions to Jane Austen and Edith Wharton novels demonstrating parallels with the sorts of social challenges faced by baboons and humans. This is primatology at its best.

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The First Boat People. By Steve G. Webb. xviii + 316 pp. Cambridge, England: Cambridge University Press. 2006. \$120.00 (cloth).

The human colonization of Australia is a topic that has engendered considerable debate over many years. This book tackles the subject with careful examination of available evidence balanced with theory, to arrive at a model for entry into Sahul well before the accepted 60 ky, perhaps even 150 ky, with the likelihood of multiple migrations during the Upper Pleistocene. Webb has probed the difficult questions of palaeodemography, possible processes of migration into Asia, Sunda and within Sahul during and between glaciations and resulting environments. He assesses ideas of "early" migration and a fit with available archaeological evidence and the physical anthropology of modern people in the region of Australia. The book provides a challenge to the "recent Out of Africa" (ROA) view currently held by many, that all modern humans are descended from a wave of anatomically modern humans that left Africa relatively recently, replacing existing hominin groups in Eurasia. This model has been largely supported by mitochondrial DNA (mtDNA) studies, and it is unfortunate that the body of mitochondrial data has not been considered. Given the title and aims of the book, the reader might be disappointed at the lack of an appraisal of the mitochondrial and Y-chromosome stories. Webb's own area of expertise is evident, but a discomfort with molecular data is also apparent. For instance to say that mitochondrial studies do not seem to consider morphology, behavior or the "human condition" (p. 59) indicates a lack of familiarity with current progress in molecular genetics. Understanding complex molecular pathways to elucidate how genes influence morphology is still a considerable distance away, despite some progress and will not be learned directly from mitochondrial studies. However, the mitochondrial data from Australia and near neighbors already provide evidence of deep, ancient maternal lineages in Australia that might support Webb's view if processes and rates of mitochondrial evolution are better understood in the future. Still, this omission does not detract from the commendable detailed analysis of a range of material that readers interested in biological anthropology and the settlement of Sahul will find extremely valuable.

Chapter 1 sets the scene to explore palaeodemography, firstly reviewing the distribution of hominins that gives some demographic parameters from which to explore possible population densities over the last 2 my. Thankfully, Webb does not enter the "species" argument with regard to earliest African fossils, simply referring to the hominins who moved out of Africa as "erectines." What is known about erectine biology is explored which is fundamental to understanding adaptation and survival, thence dispersal into Asia of erectine groups. The presence of hominins in Asia and Indonesia is accepted by 1.9 my. Evidence from Flores is important no matter how one views the debate regarding the "hobbit" skeletal material, because implements are found in deposits

dated to 50 ky, therefore establishing a hominin presence on an island that required a significant sea crossing. Extending the discussion beyond the evidence, legitimate for the aims of the book, allows Webb to speculate about the capabilities erectines must have possessed to disperse and live successfully in differing habitats, including equatorial regions (Indonesia, by 1.9 my). The reader can follow various methods that are used to estimate likely migration processes (chain of bands, pulsing waves) that could predict Pleistocene population growth (Chapter 2) from "two main population generators" (p. 62), India and China, and reasons for the genetic barrier between (Map 2.2, p. 68). The detail is important, because it leads the reader to understand why Webb proposes that populations of capable erectines must have been larger than often accepted. If so, the question arises, is the notion of "replacement" of erectines by modern humans realistic? Surely gene flow into the modern gene pool was likely, yet we are so far unable to pick it up in genetic studies.

Population growth in southeastern Asia and the region of India would provide context for population expansion, accompanied by further cultural and biological adaptation into other regions including Sunda, thence Sahul. Possible migration processes and routes to (Chapter 3) and within Sahul (Chapter 4) are suggested. Here the discussion acknowledges traditional stories regarding presence on the continent as well as indigenous concerns regarding science, an important message for readers. Webb reevaluates writings of early scholars and considers a range of current scientific evidence within Australia that shows widespread dispersal of humans. The main focus is on two key regions with which he has had extensive experience, the Lake Eyre region in central Australia (Chapter 5) and the Willandra region of western New South Wales (Chapter 6). Description of likely environmental conditions in the Lake Eyre region during glacial maxima is followed by discussion of megafaunal remains from the region, important because of the continuing debate regarding the possible role of humans in their demise ~65 kya. By extension, a role for humans in extinctions in central Australia has to assume a human presence there before 65 ky. Tantalizing glimpses of just that appear in the archaeological record and are being studied further. Webb discusses the likelihood of a mixture of influences including climate change and human behavior that might have caused extinction of megafauna.

Discussion of the Willandra people centers on the long-standing debate regarding contrasting morphology exhibited by the large collection of skeletal remains and whether or not this represents separate incoming populations. Chapters 7 and 8 deal with theoretical models of origins and time frames, by now set into a cogent matrix of available evidence. Webb asserts that "robust" characteristics probably derived from *Homo soloensis* (Java) who arriving first, followed by "gracile" immigrants during the Upper Pleistocene, subsequently adapting and mixing within Australia over a long time to produce a recognizable Australian morphology. The debate is not resolved but these questions need to be reexamined with support from firm dates if the argument for "early" arrival is to be sustained.

The reader is left to ponder these ideas and the young researcher should be stimulated, conscious of the impact they can make upon the endeavors and lives of both scientists and descendants of the people who arrived on this continent so long ago. It is hoped that by working together, that new evidence will enrich the heritage of the first Australians whose skill and adaptive abilities allowed dispersal into a wide range of habitat very early in the human story. The book is welcome, provocative and timely.

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Molecular Nutrition and Genomics: Nutrition and the Ascent of Humankind. By Mark Lucock. xii + 140 pp. Hoboken, NJ: Wiley-Liss. 2007. \$80.00 (cloth).

The scientific community has “rediscovered” that nutrients affect the expression of genetic information in an individual and individuals may metabolize and respond differently to nutrients and bioactives. This reawakening is referred to as nutrigenomics or nutritional genomics. Nutritionists have shown a great interest in applying the technologies of simultaneously analyzing thousands of genes (or variants of genes—genomics), tens of thousands of mRNAs (transcriptomics), hundreds of proteins (proteomics), and hundreds to thousands of metabolites (metabolomics). The use of these technologies promises to provide not only a detailed analyses of how chemicals in food alter genetic expression and how metabolism of nutrients may differ among each individual but also a deeper understanding of how gene–nutrient interactions maintain health or produce disease. Mark Lucock has attempted to provide an educated lay perspective of the concepts of molecular nutrition and genomics in *Molecular Nutrition and Genomics: Nutrition and the Ascent of Humankind*. Such surveys are notoriously difficult because of the breadth of the fields of nutrition, molecular biology, and genetics. Lucock uses black and white versions of Powerpoints from lectures to skim not only these disciplines but also aspects of anthropological evolution, specific “hot topic” nutrients (lycopenes, resveratrol, etc), food toxins, and technologies. The resulting survey is a “mile wide and an inch deep,” unsatisfying to the expert and overly confusing to the interested public. An example to illustrate this critique is the discussion of BMI (body mass index). A BMI of 25–30 is associated with symptoms of obesity and type 2 diabetes in Europeans and their descendants, but Asians and Native Americans (and perhaps other ancestral backgrounds) show these symptoms with a BMI of 21–23 indicating that there are gene–environment interactions that produce different physiologies based on genetic ancestry (and is reviewed in a separate chapter). Such lapses would not be made with a more

in-depth discussion of each of the important topics of nutritional genomics. The challenges of explaining gene–nutrient interactions to the interested public remain.

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From Embryology to Evo-Devo: A History of Developmental Evolution. Edited by Manfred D. Laubichler and Jane Maienschein. viii + 569 pp. Cambridge, MA: The MIT Press. 2007. \$55.00 (cloth).

As suggested by Stent (1968, p 390): “The first attempts to write the history of a scientific discipline often presage its imminent senescence.” In the case of evolutionary developmental biology or “Evo-Devo,” perhaps “maturity” provides a better description than “senescence.” Certainly, Evo-Devo currently has the hallmarks of a mature field, with several dedicated journals, a number of textbooks, and a National Science Foundation panel supporting research in this area. With the publication of *From Embryology to Evo-Devo*, the field also has an excellent book-length historical account, an outgrowth of a 2001 Dibner Seminar in the History of Biology and a subsequent Dibner Institute workshop. This interesting and timely text begins with two introductory chapters, while the remaining 14 chapters are organized into three sections as described below.

The introduction by Laubichler and Maienschein describes the lengthy gestation of this volume, and its structure and goals. By including contributions from both philosophers and biologists, the editors hope to bridge the gap between these disciplines. The historical account focuses on the relationship between ontogeny and phylogeny—as it has been studied for the past 150 years and as it is studied now. The brief “housekeeping” introduction is followed by a more conceptual and epistemological introduction by Laubichler entitled, “Does history recapitulate itself?” Laubichler introduces a variety of themes that have emerged from previous historical discussions of Evo-Devo. These include, for instance, Haeckel’s biogenetic law, the early 20th century decline in studies of evolutionary morphology, the simultaneous emergence of other disciplines, the perceived deficiencies of the modern synthesis, and ultimately the late 20th century reawakening of interest in evolutionary developmental biology. This reawakening can be seen as occurring in three phases similar to those that Stent (1968) uses to characterize the field of molecular biology: “romantic, enthusiastic, and academic phases” (p. 22). These historical themes introduced by Laubichler serve as the basis for more detailed investigations in later chapters. Laubichler also points out that given the different research programs of modern Evo-Devo—involving different goals and methods—and

the ongoing nature of this history, it is impossible to “know how the story will turn out” (p. 15). Thus this is not expected to be a definitive history, but rather a sort of philosophical interlude, reflecting where the study of ontogeny and phylogeny once was and where it is now.

In the first section, “Ontogeny and phylogeny in early 20th century biology,” five chapters provide fresh perspectives on these early studies. Fred Churchill examines Haeckel’s biogenetic law from its early roots to its later “hardening” (p. 41). The strong and weak versions of the biogenetic law are then traced through embryology textbooks in the late 19th and early 20th century. Stuart Newman shows the complexity of William Bateson’s views during the same time period. Though hindered by primitive technology, Bateson emerges as a pioneer of modern systems biology (Newman, 2003). Jane Maienschein focuses on cells as objects of study and introduces a number of themes that characterized the developmental biology of the early and mid-20th century. Maienschein complements Newman’s elucidation of the subtlety and complexity of biological thought during this period. Garland Allen takes an explicitly dialectic view of the early study of ontogeny and phylogeny. Such a view seems appropriate for the contrasting styles of evolutionary morphologists (e.g., more observational and synthetic) and experimental embryologists (e.g., more experimental and analytic). Marsha Richmond concludes this section with a detailed discussion of Richard Goldschmidt’s efforts to maintain a unified view of development and evolution during this time. The important role of model organisms in general and Goldschmidt’s model (gypsy moths) in particular is highlighted.

In the second section, “Roots and problems of evolutionary developmental biology,” six chapters focus on the early to mid-20th century when studies of evolutionary morphology showed at least a relative decline but at the same time the roots of modern Evo-Devo became apparent. John Wourms provides an encyclopedic documentation of the field of comparative evolutionary embryology in the US. He traces the influence of Louis and Alexander Agassiz and the development of institutions favorable to organismal studies. He suggests that two embryologies coexisted throughout the 20th century and that comparative and evolutionary studies survived to give rise to Evo-Devo. Alan Love pursues complementary themes, but from a more focused perspective. By using the work of Dwight Davis and William Gregory as exemplars, he shows that the themes of Evo-Devo are based on deep roots in the 20th century. Davis’ work is particularly noteworthy because SJ Gould, shortly after the widely acknowledged landmark *Ontogeny and Phylogeny*, highlighted Davis’ studies of the panda’s thumb as a compelling example of the contingent nature of adaptation. William Wimsatt more generally discusses internal factors in evolution, focusing on critiques of the modern synthesis by Lancelot Law Whyte, Rupert Riedl, and later by Wallace Arthur. Riedl’s views are particularly fascinating (e.g., “evolution as a series of layered contingencies added to development,” p. 322). Riedl’s influence on modern Evo-Devo undoubtedly would have been greater but for a tendency to mix philosophy and biology at a time when this was particularly unpalatable for many empiricists. Scott Gilbert provides a short chapter illuminating the connection between embryological fate maps and more recent studies of gene expression. James Griesemer examines the early 20th century split between embryology and Mor-

gan’s transmission genetics. He delves into Mendel’s work to illustrate that this split was not inherent in the science of genetics, but rather a later “foregrounding” of certain aspects of this work. The statistical irregularities of Mendel’s data, first pointed out by RA Fisher, might have been worth mentioning in this context. Part II concludes with a chapter by Elihu Gerson, again tackling one of the central questions of this volume, “How did the separation of two lines of research come about? What happened to bring them back together” (p. 435). In this context, Gerson focuses on institutional and technological developments that favored certain styles of research at different times in the 20th century.

In the final section, “Reflections,” three chapters provide points of view from leading practitioners of modern Evo-Devo. Brian Hall describes this field within a historical framework. This history shows that Evo-Devo has always been approached from a variety of conceptual perspectives. For 19th century embryology, Hall also highlights institutional and instrumental advances such as the Naples Zoological Station and the automatic microtome. Gerd Müller takes a more contemporary point of view. He notes that while Evo-Devo seems to be becoming a distinct discipline, “surprisingly different accounts of the origins, the contents, the aims, and the significance of this nascent discipline are being told” (p. 499). He provides six memos—history, concepts, agenda, method, explanation, integration—that characterize Evo-Devo as a distinct discipline. In the final chapter of this section, Günter Wagner also recognizes the present day disunity of Evo-Devo. He points out the risks for a scientific field that cannot agree on standards of evidence. In this context, Wagner suggests that microevolutionary approaches may be valuable and concludes with an example using neutral networks to study phenotypic evolution.

This stimulating and comprehensive volume will no doubt elicit further efforts from philosophers and further reflections from evolutionary developmental biologists. As one of the latter, I wonder if some of the answers to the questions “Why not before, and why now?” (p. 109) are too briefly explored. Perhaps JP Trinkaus has a point: “Hell no, we [developmental biologists] didn’t feel left out of anything. They [evolutionary biologists] were just jealous because they couldn’t figure how to get the NIH funding!” (p. 109). On the other hand, the record of modern, reductionist biology in making successful predictions (e.g., the number of genes in the human genome) is modest at best. Perhaps the ongoing Evo-Devo synthesis can better this record.

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The Origins of Genome Architecture. By Michael Lynch. xvi + 494 pp. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers. 2007. \$59.95.

Massive augmentations in genome-size and in genomic embellishments took place with the evolutionary transitions from prokaryotic organisms (bacteria and archaeobacteria) to single celled eukaryotes (paramecia and amoebae), and then to multicellular eukaryotes (plants, fungi, and animals). Multicellular eukaryotic genomes are typically more than 10 times larger than prokaryotic genomes and are extraordinarily baroque structures: embellished with genes containing multiple regulatory elements and interrupted by introns, saturated with mobile genetic elements, and filled with vast intergenic regions. Many of these embellishments contain elements that play important adaptive roles today, but was this so when they originated? Is it necessary to invoke natural selection as the originator and initial propagator of these genomic embellishments? These are the central questions addressed by Michael Lynch in his new book, which presents a synthesis and extended treatment of his research over the past 25 years. Lynch examines each genomic embellishment in turn demonstrating how the constraints imposed by natural selection would have, in fact, curtailed their emergence, and how nonadaptive evolutionary forces were necessary for their origin.

Lynch argues that any explanation of genome evolution should be consistent with established population genetic principles. One fundamental principle Lynch explores is how population size influences the balance of evolutionary forces acting on new variants (in this case genomic novelties). While such analyses will be challenging for many biologists, they are accessible especially with textual interpretation. The key point is that as populations become smaller in size, genetic drift can play a role that dominates over natural selection in determining the fate of new variants. In contrast, as populations become larger in size, natural selection becomes the increasingly dominant force in either promoting advantageous or removing deleterious new variants. These ideas were formally developed by Motoo Kimura and Tomoko Ohta in the 1970s. Their theory describes that while a mutation may be moderately deleterious in a large population and removed by purifying selection, the same mutation can be “effectively neutral” in a small population where it may ultimately become fixed by genetic drift. Though this theory has been available for over 30 years, Lynch argues that most researchers of genome evolution and of biological phenomena more generally largely overlook or ignore it, invoking natural selection instead.

Lynch explains how each embellishment added to a genome increased its vulnerability to deleterious mutations, leading to the expectation that it would be eliminated by purifying (negative) selection. For example, each embellishment (e.g. intron, transcription-factor binding site, and untranslated flanking region) added to a gene would increase its vulnerability to inactivation. Likewise, each mobile genetic element (e.g. transposon, retrotransposon) inserted into a genome does so indiscriminately with respect to genes and would often have deleterious effects. Therefore, to explain how these embellishments became preserved and then fixed in genomes by *positive* natural selection becomes problematic. However, Lynch shows us

that it is possible to quantify the negative selective coefficients associated with most genomic elements arising in a population, and to evaluate these costs with respect to the balance of evolutionary forces acting in the population dependent on its size. The population sizes of prokaryotic species are estimated to be several orders of magnitude larger than population sizes in eukaryotes; and population sizes in multicellular eukaryotes are even more reduced. Thus, Lynch argues that when many genomic embellishments arose within eukaryotes they fell into an “effectively neutral” class and therefore owe their origin and initial spread to the random effects of genetic drift. In other words, the relaxation of natural selection in eukaryotic species has provided the central mechanism permitting increasing genomic embellishment. In contrast, the relative simplicity of the genomes of prokaryotes is an indirect consequence of the barrier to the passive emergence of genomic complexity imposed by large population size and increased effectiveness of natural selection.

So, in Lynch’s view, did *adaptive* natural selection play a part in the evolution of genome complexity? The answer is, well, hard to tell. Lynch describes that sometime after the prerequisite “neutral transition” zones, the embellishments that were successfully added to the genome became substrates positive selection could act on. In Chapter 10, Lynch convincingly describes how systems of gene modularity (the ability to regulate gene expression in different tissues, developmental stages, and environmental contexts) could have emerged by nonadaptive processes in multicellular eukaryotes. Certainly, many such features play adaptive roles in organisms today. Unfortunately, Lynch has not led us to the evolutionary moments or contexts in which positive selection became important in driving adaptive changes within these systems. However, he does indicate that the relaxation of pleiotropic constraints could have been an early adaptive benefit of modularity. Lynch addresses the issue somewhat more when considering gene duplications and intron insertions. After describing intricate (yet plausible) ways by which these elements could establish footings in the genome by nonadaptive processes, several ways are described by which they could be subsequently adaptively exploited. For example, introns seem to play adaptive roles in a cellular process that removes truncated mRNA transcripts resulting from premature termination codons. For gene duplicates, following an initial nonadaptive origin via subfunctionalization (in which duplicates are preserved in populations of small size), later adaptive processes can lead to them evolving novel functions. While Lynch’s explanations of the nonadaptive origins of genomic complexity are extremely thorough and convincing, his descriptions of how adaptive evolution may have played subsequent roles are not as thorough. Thus, we are left in doubt about how, and to what degree, natural selection has played a role in the evolution of genome complexity, and by extension organismal complexity.

This is a dense and complicated book that presents an important unifying theory of genomic diversity. Lynch has convincingly shown that in analyzing evolutionary questions: the “quantitative details matter!” Quantitative evaluation helps us understand the relative influence of various evolutionary forces—natural selection, genetic drift, mutation pressure and recombination—on genomic evolution. Moreover, we learn to appreciate how the three latter nonadaptive forces can often play dominant roles. (Of par-

ticular interest to human biologists is a short section describing how long-term small effective population size in the human lineage has elevated nonadaptive processes in our evolution.) The book incorporates a generous quantity of color figures (mostly graphs) and tables that help to elucidate relationships between genomic embellishments and genomes across phylogenetic groups. The book (and its comprehensive bibliography) will be a useful reference source for genetic researchers, and will serve well as a textbook for upper level courses in evolutionary genomics or evolutionary genetics. Finally, Lynch's emphasis on nonadaptive explanations is extremely important and pro-

vides a much needed counterbalance to adaptive explanation in biology.

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