

understanding of the origin of the asymmetry between matter and antimatter in the universe, based on grand unified theories, and a method for addressing the classical questions of why the universe is so uniform and its spatial geometry so flat, based on the idea of inflation. In the early 1980s the problem of the quantity and nature of the invisible mass that seems to dominate the gravitational universe and the related problems of the formation of large-scale structures and the distribution of galaxies have sharpened both theoretically and observationally. In addition, important data on the relative abundance of the very light isotopes ^1H , ^2H , ^3He , ^4He , and ^7Li , believed to be synthesized in the first moments of the big bang, on the anisotropies—or lack thereof—in the microwave background radiation, and on the distribution of galaxies are accumulating continuously.

It should also be remarked that the very early universe and the relics it leaves are the main domain of application of modern particle physics to understanding the natural world (as opposed to understanding elaborate experiments at accelerators; a possible exception is that when neutrinos from the sun or from supernovae are observed, their intrinsic properties can affect the interpretation of the observations).

Altogether, then, the topic chosen for the first school is an important one with continuing vitality. How well does the volume cover it? On the whole, in this reviewer's opinion, very well.

The volume includes three minicourses by James Gunn, Stephen Hawking, and Michael Turner. Gunn's course starts with a breezy introduction to the standard Friedmann models and their classical consequences for large-scale kinematics and cosmic ages. This is followed by an elementary account of the theory of formation of large-scale structure and of galaxies. The exposition, which touches many of the main issues with a maximum of intuition and a minimum of formalism, will be especially valuable to students. There is, in these notes, a refreshing directness and emphasis on practical issues of observation.

Whereas Gunn's lectures might be said to deal with "classical" cosmology, Turner's course—at 114 pages, more than half the book—deals with "modern" cosmology, where microphysical considerations are essential. Nucleosynthesis, matter-antimatter asymmetry, inflation, and the issue of invisible matter are introduced in detail. In addition, Turner discusses magnetic monopoles. Since they should have been produced at sufficiently high temperatures in the early big bang, their apparent nonexistence (or at least, extreme rarity) is a puzzle—solved,

perhaps, by inflation. Finally, Turner gives a substantial discussion of axions, one of the leading contenders for the role of invisible matter. The microphysical reasons to believe in their existence, their production in the early universe, and the possibilities for their observation are all discussed. In this last regard, it is worth noting that if the new high-temperature superconductors fulfill their promise of delivering large magnetic fields over substantial volumes, the search for the axion background will become an optimistic enterprise.

Hawking's lectures deal with issues arising in quantum gravity—"post-modern" cosmology. Fundamental questions are raised: How is the wave function of the universe to be interpreted? Probabilistically, presumably—but what does probability mean, for the universe as a whole, since a frequency interpretation is clearly inappropriate? What boundary conditions are to be imposed on the universal wave function? After all, boundary conditions usually set the parameters of the influence of the external world, or the past, but here there can be no retreat. Such questions, as they arise in quantum gravity, are treated briefly but with elegance and lucidity. Whether work along these lines will yield observable consequences, or indeed survive revisions in our thinking about the nature of gravity in the ultraextreme conditions where its quantization matters, remains, however, an open question.

In summary, the first volume is a fine addition to the pedagogical literature, and I recommend it highly to student and expert alike.

The second volume, *Physics in Higher Dimensions*, is in my opinion considerably less successful. Given the subject matter, whose central core is rather murky, this was perhaps inevitable. Indeed, the mainstream of

speculations on higher-dimensional physics has since shifted in directions that are only hinted at in this volume.

There are written versions of five minicourses in the second volume. Two of these, by Raoul Bott and Steven Weinberg, are essentially mathematical. The lectures by Bott present, in less than 40 pages, a slice through homotopy theory, de Rham cohomology, and characteristic classes. I think it would be very difficult for most physicists to learn the material from these notes alone, especially because of the sparsity of concrete examples or applications. Weinberg presents an account of what mathematicians call the local theory of G -structures—a generalization of Riemannian geometry. Although the ultimate utility of this material for physics is most unclear, it is presented with the author's usual clarity and explicitness.

Michael Duff's lectures on Kaluza-Klein theory reflect the author's obvious enthusiasm for the subject, but a beginner may find his rapid descent into intricate details of model building disorienting. Christof Wetterich, on the other hand, presents a brief but penetrating exploration of just two comparatively sharp issues in Kaluza-Klein theory: the origin of chirality and the possibility of noncompactness in the hidden dimensions.

John Schwarz's lectures provide a brief but brilliantly clear introduction to superstring theory. This theory has come to dominate recent thinking about higher dimensions and more general speculation about high-energy physics beyond the standard model. Schwarz's lectures in this volume will be a useful entrée for physicists curious about this exciting but notoriously difficult subject.

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Travelers and Their Fate

Ecology of Biological Invasions of North America and Hawaii. HAROLD A. MOONEY and JAMES A. DRAKE, Eds. Springer-Verlag, New York, 1986. xviii, 321 pp., illus. \$59. Ecological Studies, vol. 58. Based on a symposium, Asilomar, CA, Oct. 1984.

Ecology of Biological Invasions. R. H. GROVES and J. J. BURDEN, Eds. Cambridge University Press, New York, 1986. xii, 166 pp., illus. \$42.50. Based on a symposium, Canberra, Australia.

Quantitative Aspects of the Ecology of Biological Invasions. HANS KORNBERG and M. H. WILLIAMSON, Eds. Royal Society, London, 1987. First published as *Philosophical Transactions* of the Royal Society, series B, vol. 314, pp. 501–572. £43. From a meeting, London, Feb. 1986.

Throughout most of the world, species have been purposely or accidentally introduced from one region to another, often with enormous economic and medical con-

sequences. SCOPE, the Scientific Committee on Problems of the Environment, chartered symposia in North America, Australia, and Britain to deal with three main ques-

tions: What factors determine whether a species will become an invader or not? What site properties determine whether an ecological system will accept or repel invaders? And, given answers to those questions, how can we best manage ecological systems to avoid problems? Answers to this set of questions are important not only with respect to management issues but also for understanding how natural systems work. This dual significance is a recurrent theme throughout the three volumes resulting from the SCOPE symposia (to be designated here as NA, A, and B, respectively).

While purposeful introductions have probably been going on since humans invented culture, they had a heyday in the late 1800s when "Acclimatization Societies" were established in former colonies (the United States, Hawaii, New Zealand, Australia, the Society islands, and the Mascarenes, among others) with the sole purpose of introducing new species to their faunas and floras, which were perceived as depauperate. The records kept by these societies were often meticulous, allowing G. M. Thomson, as early as 1922, to synthesize the changes wrought in New Zealand in *The Naturalization of Plants and Animals in New Zealand*. Such purposeful introductions offer the kind of "experiments" that are necessary to test theory but that today would be impossible because they are illegal if not immoral. True, no precise controls or replicates were present; true, as with all historical work, we must often rely on the sometimes conflicting accounts left us by different deceased actors and observers; but the vast numbers of species and locations involved, together with the ability to conduct present-day surveys in these same places, present opportunities to untangle many interwoven variables affecting the very core of controversial issues in ecology, evolution, and biogeography.

One important ecological issue is whether natural communities vary in their resistance to invasions because of intrinsic properties of the natural system. The ancient Greek and Roman concept of "a balance of nature" was based in part on the observation that population explosions, dramatic range expansions, and plagues are not as common as they might be (F. Egerton, *Quart. Rev. Biol.* **48**, 322 [1973]). In his landmark book of 1958, *The Ecology of Invasion by Animals and Plants*, Charles Elton examined the question of geographic invasions in more quantitative detail and concluded that species-poor sites like isolated islands or artificially species-poor habitats like agricultural and urban habitats were less resistant to invasions than species-rich and undisturbed areas.

The Eltonian legacy is strongly felt in

these three volumes (see for example chapters by Orians [NA], Moulton and Pimm [NA], and Fox and Fox [A]). Moulton and Pimm show that the more bird species present in a community the less likely a bird species is to invade successfully; moreover, the more morphologically similar it is to the residents, the worse its chances are. Such effects may not be evident in other taxa. In a provisional analysis of the vast data set from arthropods introduced for biological control purposes, Simberloff (NA) finds no support for the proposition that island systems are more accepting of exotic insect invaders than are mainland systems. Yet, as he cautions, "Most biological control efforts on mainland or islands are in agricultural communities, and these may be more similar to one another than would be pristine communities." Also, as Simberloff points out, testing Elton's hypothesis can be tricky. Simply taking species lists and plotting the number of exotics as a percentage of total species (as the y -variate) versus the number of native species today (as the x -variate) will not do. Any inverse relationship between the two variates (such as that shown by Fox and Fox [A] for Australian plants) can simply be a statistical artifact of including the x -variate in the denominator of the y -variate.

A less controversial site-specific factor affecting success is the requirement that the habitats and climates be similar in the old and new homes. Yet it is surprising that such habitat matching often provides little predictive value. Bird species introduced to tropical Hawaii from tropical areas do not differ from those introduced from temperate areas in their chances of success (Moulton and Pimm, NA). Similarly, one of the most abundant introduced lizards on Hawaii is the skink *Leiolopisma metallicum*, which comes from the cool temperate areas of Tasmania and adjacent Victoria, Australia, and is thought to be responsible for reducing the occurrence of the skink *Emoia cyanura* introduced earlier by Polynesians. In a broad taxonomic analysis of British introductions, Williamson and Brown (B) conclude that climate matching is "far from all-important."

Introduced species also offer important opportunities to test evolutionary theory. According to the idea of evolution via "punctuated equilibria" the conditions for rapid speciation occur when a few individuals find themselves in a remote and foreign environment. These are exactly the conditions that many introduced species have faced, and one obvious question is whether much speciation has occurred in the intervening time. The answer seems to be a profound *no*, although the question is not explicitly addressed in these books, as it lies

outside their charter. Another related question is: Do the successful species differ from the failures in their genetic properties? Unfortunately, as Gray (B) and Barnett and Richardson (A) observe, it is difficult to separate the effects of the invasion process (a bottleneck in population size, forced inbreeding, and so on) from features that might preadapt species to be invaders.

Insights into the importance of coevolution in molding natural communities can be gained by comparing natural communities with artificially constructed ones via introduced species. All organisms must gather food (or, in the case of plants, nutrients and light) and at the same time are in danger of being gathered as food by species at higher trophic levels. In different places with different evolutionary histories, species should evolve somewhat different trophic adaptations; how specific these will be to the particular set of species they interact with is an open question. Will a native predator be better at catching exotic prey than native prey because the exotic prey have not evolved adequate defenses to these predators? Or will the reverse be true because these predators have not evolved the unique traits necessary to hunt the exotic? Pimentel (NA) presents some important data: weeds of vegetable crops (which are nearly all exotic plants) consist primarily of exotic species. Herbivorous insect pests of the same U.S. crops studied by Pimentel are, on the other hand, dominated more by native species, as are pests of the U.S. forests. One conclusion is that for weedy plants the problems of new and different resources are more than compensated for by their release from the native herbivores and parasites of their homeland. Native herbivorous insects also have not had trouble adjusting to novel foods. In spite of the fact that they are attacked by a richer fauna of predators and parasites, they are often more successful than their exotic counterparts with a longer history of feeding on the same crop plant. One conclusion is that the few native enemies that do attack these insect invaders do so with great voracity. An important evolutionary conclusion is that coevolution might result in an asymmetry: an enemy can fare better with a novel prey than a prey with a novel enemy. Pimentel is quick to point out an important practical message: rather than search for biological control agents in the homeland of an exotic pest perhaps we should try importing enemies that have no evolutionary history with that pest as a host.

In a similar vein, much can be learned about the amount and direction of coevolutionary systems by studying the fate of host and microbe in exotic disease systems such

as myxomatosis disease in introduced rabbits (Ross and Tittensor, B; Gibbs, A) and a host of other diseases aptly examined by Anderson and May (B) and Dobson and May (NA).

The history of introduced species suggests some obvious places where ecological theory could be improved. Roughgarden (NA) reviews the theory relating the rate of spread of a successful invader. This theory predicts that the radius of the invader's geographic distribution should increase linearly with time, and Roughgarden comments that "the theory . . . is quite robust, has been empirically tested, and is about as reliable as theory gets." But how long will this relationship hold? In a number of situations areal spread of an invader remains stable for long periods of time for no apparent reason. In Eurasia the tree sparrow has a range almost as large as that of its congener, the house sparrow. Unlike the house sparrow, which has spread throughout most of North America, the tree sparrow after being successfully introduced to the St. Louis region in 1870 never expanded much beyond that immediate region (Ehrlich, NA). A number of successfully introduced birds and lizards are likewise confined to the Dade County region of Florida and have been for quite some time. Suddenly, and for no obvious reason, species sometimes break out of their geographic bounds. The collared dove, *Streptopelia decaocto*, spread from the Balkans to occupy most of Europe by the 1970s (O'Connor, B). It is interesting that most of the deviations from the "areal radius grows linearly with time" rule appear to be continental examples, and this needs more empirical verification.

These three volumes are each well edited, and the choice of authors and subjects is superb. Because they are symposium volumes the level of integration between chapters is not that of a one-authored book, but the North American and British volumes each have at least one synthetic chapter that attempts to put the entire volume in perspective. In addition, chapters by Williamson and Brown (B), Groves (A), Myers (A), and Mooney *et al.* (NA) have an encyclopedic scope.

There are some differences in emphasis among the volumes. The British volume deals less with community-level factors than the other two; the Australian volume emphasizes more practical management issues. Together the regional orientations of the volumes make them a welcome complement to the growing number of taxon-specific books (such as John Long's *Introduced Birds of the World* and Christopher Lever's *Naturalized Mammals of the World*).

More often than not, issues in population

biology will not be resolved by the single critical experiment: the nut doesn't crack, as it often does in molecular and cellular biology, but rather is slowly ground away with the weight of accumulated evidence. Our understanding of natural communities and our ability to predict invasions may not go hand in hand. Yet the urgency of these issues grows as we gain the technological skills to create genetically engineered organisms (Regal, NA). These three volumes will be indispensable in grinding the nut of important issues encompassed by the history of exotic invaders.

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Island Birds

Ecology and Evolution of Darwin's Finches.

PETER R. GRANT. Princeton University Press, Princeton, NJ, 1986. xiv, 459 pp., illus., + plates. \$55; paper, \$22.50.

The geospizine, or Darwin's, finches of the Galapagos archipelago have figured prominently in the development of evolutionary and ecological theory. On the basis of Darwin's original observations and arguments, as modified by various workers, especially David Lack, they are cited in biology textbooks as illustrating adaptive radiation, the effects of interspecific competition, speciation processes, and related phenomena. Until recently, however, most of the information on these finches, including that provided by Darwin, was based on brief field

studies or analyses of museum specimens.

Now Peter Grant, in this beautifully produced and clearly written book, summarizes the first long-term field studies of finch populations in the Galapagos, conducted by himself and his students and colleagues over the last 10 to 15 years. The resulting data are interpreted in light not only of the ideas and speculations of previous workers but of modern ecological and evolutionary theory. Well-designed field studies and analytical procedures provide data supporting the allopatric model of speciation, the importance of interspecific competition, the adaptiveness of intraspecific morphological variation, and the ongoing process of natural selection on morphological traits. These and related topics are integrated into a coherent discussion of the ecological and evolutionary processes that have influenced, and are still influencing, the diversification of this group of organisms. The picture is by no means complete, and Grant is quick to point out where there are weaknesses in his arguments and where more data and experimentation are needed.

The book is organized in four sections: an overview of the Galapagos Islands and of the finches; a treatment of finch morphology, including intra- and inter-specific variation and growth patterns; an account of finch ecology and behavior, with emphasis on feeding relations, mate selection, and breeding; and a discussion of finch evolution and diversification. In these areas Grant and his associates have made significant contributions.

The 14 currently recognized species of geospizine finch are extremely variable in morphological characteristics, a feature that both intrigued and confused Darwin. Grant shows that the greatest differences within populations and between species are in beak dimensions. These are apparent shortly after hatching but become exaggerated through differential allometric growth. Through field observations of feeding behavior and diet of selected species on several islands, he demonstrates that bill size and shape influence the range of food types eaten by the finches. This occurs between populations of the same species on different islands and even among members of a single morphologically variable population (*Geospiza fortis* on Santa Cruz Island). Thus, intra- as well as inter-specific differences in bill morphology affect the efficiency with which these birds exploit available foods.

The significance of these findings is enhanced by the documentation that food is often the factor limiting population size for these finches. Although direct experimental manipulation of food supplies or of the birds was not possible, Grant provides convincing



"Woodpecker finch, *Cactospiza pallida*, using a tool [here a twig] to extract insect larvae from a dead branch of *Bursera graveolens*." [From *Ecology and Evolution of Darwin's Finches*; photograph by R. Perry]