

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]

correlational evidence that food limitation occurs in the late dry season of many (if not most) years. At a minimum, it seems to occur at least once per finch generation.

Furthermore, by obtaining morphological measurements from populations of *G. fortis* on Daphne Major over a series of years during which drought and feeding conditions varied, Grant and his students were able to document the differential survival of certain phenotypes and to relate the differences to ecological events. In this case, individuals with larger body size and greater bill depths survived better than smaller individuals. This was correlated with the presence of larger and harder seeds, which larger birds were shown to handle more efficiently. The differential survival of large phenotypes was shown to be further enhanced by females' choosing larger males when selecting a mate. Grant estimates that the combined effect of natural and sexual selection in this event resulted in a 4 to 5% shift in the direction of larger size in the population. Counterpressures on size and other characteristics are also considered, as are additional factors that influence evolutionary change in these species, such as sexual selection, hybridization, and genetic drift.

Grant concludes the book with a synthesis and his current view of the ecological forces and evolutionary processes that have led to the diversification of Darwin's finches. Although some of his views are clearly supported by data and experimentation, others still require verification. This is particularly so with respect to the generality of the findings. Grant's work thus far has concentrated on the more common species of ground finches (*Geospiza*), mainly on two or three islands. Since manipulative experiments cannot be conducted in the Galapagos, further long-term studies comparing population processes of the same and different species on different islands, as well as information on the other finch species, especially the tree finches and the warbler finch, will be necessary.

Likewise, studies of the relationship between finch morphology and behavior (functional morphology) are needed to substantiate claims made on largely circumstantial grounds. And, as Grant points out, the application of recently developed biochemical and genetic techniques might provide new ways of assessing the genetic affinities and relationships among the finch species and their possible ancestral stocks in Central or South America.

The most impressive feature of the current work, however, is the quantity and quality of the data and ideas that have been generated from intensive, well-designed, and relatively long field studies of natural

populations. Population geneticists, evolutionists, ecologists, and indeed anyone interested in biology and the diversification of organisms will find interesting and provocative material in this book. They will also find the writing clear, the procedures and rationales of the analyses explicitly stated, and the photographs of the finches and their islands superb. This book is destined to become a classic in the field of ecology and evolution.

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## Suspended Animation

**Metabolic Arrest and the Control of Biological Time.** PETER W. HOCHACHKA and MICHAEL GUPPY. Harvard University Press, Cambridge, MA, 1987. xvi, 227 pp., illus. \$27.50.

A common fixture of science fiction is the possession of the ability to control biological time. In contrast to chronological time (clockwork), biological time is hypothesized to be more relative and amenable to slowing or arrest. Survival during space travel or profound longevity could theoretically result from slowing metabolic processes or entering a state in which metabolism is entirely suspended and life, by most definitions, ceases until arousal. This hopeful dream is typified for me by a slogan on a panel van in our neighborhood: "Life extension through cryonic suspension."

This book reminds us that such metabolic arrest is not fantasy but is rather a daily or seasonal feature of the lives of many animals. It is not impossible or even particularly unusual. Metabolic depression is a common strategy when animals encounter temporarily inhospitable environments, those with a lack of sufficient heat, oxygen, water, or usable energy. Resources are marshaled until better times return and normal life can resume. Examples of this depression can be found in nearly all groups of animals, for example during diving in birds and mammals, estivation in snails and lungfish, freezing in insects and frogs, and hibernation in rodents and turtles. Some animals—nematodes, tardigrades, brine shrimp cysts—can enter an ametabolic state, in which energy utilization and all other functional processes stop completely and animation is suspended.

This book is the story of these animals and a summary of our knowledge of their physiology and biochemistry. It is a good book and succeeds at several levels, both in its exploration of physiological diversity and in its examination of the underlying commu-

nality of the mechanisms of metabolic depression. The authors assert that a common feature of metabolic slowdown in all these animals is the inactivation of transport channels in cell membranes. This "channel arrest hypothesis" recognizes that transport processes, particularly sodium-potassium exchange, are energetically expensive and represent a large fraction of the total energy expenditure of a cell. The temporary suspension of this transport would result in an immediate and substantial decline in energy demand. The suppression of other cell functions—aerobic and glycolytic metabolism, protein and RNA synthesis—is found more selectively and results in further energetic savings. The extrapolation of some or all of these functions to particular cases is sometimes quite conjectural, as the authors readily acknowledge. The value of their hypotheses will be seen in the widespread research that this book will surely provoke on such phenomena as hibernation, cryogenics, and anhydrobiosis. This is an excellent example of the vitality and utility of the field of comparative physiology.

While my overall assessment is very positive, the book is not without its faults. Its coverage of different animal groups is uneven. Some chapters are well-balanced discussions. Others are eclectic. The section on diving, for instance, discusses only the authors' own work on Weddell seals; that on anhydrobiosis concentrates almost exclusively on brine shrimp cysts. Though these are the best-studied examples, they are far from the only ones, and, as this book demonstrates elsewhere, much information can be obtained from diverse systems. The prose is often hard to interpret. Convolutional sentences are common, including one that is 82 words long (pp. 54–55), and difficult to follow. Technical terms are used freely, and an extensive background in biochemistry and physiology is assumed.

My only other reservation about this presentation is the complete enthusiasm with which the authors embrace metabolic slowdown or arrest. Its advantages, which are considerable, are discussed thoroughly. Its disadvantages are not. Its unspoken price is precisely the withdrawal from life that is otherwise praised. A hibernating, estivating, or frozen animal may survive, but it cannot simultaneously be fully alive. It cannot feed, behave, or, most important, reproduce. Its departure from normal metabolism is also a departure from the opportunities of normal life. It is not only biological time that is arrested; it is life itself.

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