Variability in the Tropics

The Ecology of a Tropical Forest. Seasonal Rhythms and Long-Term Changes. EGBERT G. LEIGH, JR., A. STANLEY RAND, and DONALD M. WINDSOR, Eds. Smithsonian Institution Press, Washington, D.C., 1982. 468 pp., illus. Paper, $25.

Barro Colorado Island is unquestionably the world's most active and august center for research in tropical biology. Situated in Lake Gatun in the center of the Panama Canal, the island first attracted the attention of researchers in the teens of this century, and in 1946 it was officially acquired by the Smithsonian Institution as a permanent research reserve.

Ever since the early observations of Allee, Chapman, and Enders in the 1920's, workers on the island have appreciated that the climate is markedly seasonal and that the alternation between wet and dry periods results in a profound oscillation in the availability of resources important to animals. But it was not until nearly 1970, when N. Smythe and R. Foster began their pioneering measurements of fruit fall, that resources per se began to receive proper attention. A few years later the Smithsonian launched its Environmental Sciences Program, which financed environmental monitoring activities on the island under the guidance of A. Rand. This volume is a direct outgrowth of that program.

It contains 32 chapters plus an introduction by E. Leigh, the senior editor. Seven sections cover the following major topics: the physical setting (climate, geology, hydrology), the biotic setting (vegetation), seasonal rhythms in plants (flowering, fruiting, leafing), frugivores (mammals, birds), insects of tree crowns, leaf litter arthropods, and long-term changes. Although the chapters range from extremely general to sharply focused, nearly all of them adhere closely, both in spirit and in fact, to the pervasive central theme of seasonal and year-to-year variability and its effects.

Although seasonality is clearly stronger in the temperate regions, its effects on tropical ecosystems are nonetheless profound, regulating the timing of reproduction and other critical life functions at every trophic level. What is more important from the point of view of population regulation, however, is year-to-year variability. Here it is shown in a wealth of long-term studies on a wide range of creatures from leaf litter arthropods to large mammals that the magnitude of year-to-year climatic fluctuations and the impact of these fluctuations on populations are every bit as strong as in temperate ecosystems.

Aseasonal rains in what is normally the dry season, for example, can produce disastrous consequences (chapter by R. Foster). In one such year, numerous species of trees that normally flower with the onset of the rainy season failed to flower. Consequently, the second of two major annual fruiting peaks was suppressed, and a prolonged famine resulted from August 1970 to February 1971. "Animals foraged longer, fed on novel foods, some with obvious mechanical defenses, and died in unusual numbers" (R. Foster, p. 201).

Even in normal or good years, the end of the rainy season is a time of scarcity, as indicated not only by direct measurement of resource levels but by the observation that most birds and mammals do not produce young at this time. In a few cases (for example, howler monkeys) it has been possible to document directly that mortality is concentrated in the late rainy season. At a broader level, there is widespread agreement among the contributors that the annual period of resource scarcity seems to impose a ceiling on animal numbers, by curtailing reproduction, by increasing mortality, or both.

From the various chapters one can piece together a nearly complete view of the functioning of the tropical forest ecosystem. In fact, one could argue strongly that the production and flow of resources on Barro Colorado Island are better measured and understood than in any temperate forest, notwithstanding the additional complexity that comes with tropical diversity. In contrast with more traditional ecosystem studies emphasizing plant productivity and nutrient cycling, the approach here is to assume tacitly that the system is in steady state with respect to productivity and nutrients. This being so, the focus devolves on the forest's production of food for animals and on the animals themselves. Thus, there are key chapters on leaf production and litter fall (E. Leigh and D. Windsor), rates of herbivory (P. Coley), fruit fall (R. Foster), the seasonal abundance of night-flying insects (N. Smythe), and leaf litter arthropods (S. Levings and D. Windsor).

It emerges that about 6.5 tons (dry weight) of leaves fall to the Barro Colorado Island forest floor per hectare per year. About 7 percent of the area of these leaves consists of holes or gaps representing the depredations of insect herbivores, exclusive of leaf-cutting ants. Estimates of the rates of consumption by vertebrate herbivores (around 250 kilograms per hectare per year, mainly sloths and howler monkeys) and by leaf-cutter ants (around 300 kilograms per hectare per year) add to suggest a total production of nearly 8 tons of leaves per hectare per year and a rate of herbivory of about 15 percent. (More direct and precise measurements of insect herbivory by P. Coley, however, suggest that this alone can account for more than 20 percent of annual leaf production.)

Fruit comes second in importance to foliage in the array of resources produced by the tropical forest. Measurements of fruit fall plus estimates of arboreal consumption suggest an annual production in excess of 1 ton (dry weight) per hectare per year. This production, however, is distributed very unevenly over time. Much of it comes when consumers are sated, so that nearly 80 percent of the total rots on the ground. But during the late rainy season production drops to very low levels, so that the amount of fruit falling is inadequate to meet the needs even of agoutis and pacas, not to mention peccaries and other terrestrial frugivores. During these regular annual periods of food deprivation, animals must alter their habits to survive: agoutis live on scatter-hoarded nuts, pacas browse and lose weight, and peccaries dig for roots and tubers. Accounts of the means that various species employ for surviving resource crunches provide some of the most fascinating reading of the book.

Although not all the chapters can be described as innovative or convincing, the book contains a number of highlights in addition to the central core of reports derived from the environmental monitoring program. There is an excellent series of chapters on plant ecology, dealing with such basic subjects as the history of the Barro Colorado Island forest (R. Foster), rates of tree mortality (F. Putz and K. Milton), the spatial distribution of trees (R. Thorington *et al.*), gap production (N. Brokaw), and the seasonal

rhythm of seed germination (N. Garwood). In addition, much of the strength of the remaining chapters is derived from the burgeoning botanical expertise of workers on the island, a tribute largely to the excellent recent flora by T. Croat and the patient tutelage of R. Foster.

Reports on long-term studies of animal populations constitute another major contribution. Nearly all of these clearly show the effects of good and bad years on the key demographic processes of recruitment and mortality. The most significant of these studies, on howler monkeys, goes back nearly 50 years to the work of Carpenter. The account of changes in age structure, birth rate, and age-specific mortality during periods of rapid increase and subsequent stability provides important insights into the processes regulating this population and surely constitutes the best demographic study to date of a rain forest mammal (K. Milton).

I have intentionally concentrated on strengths in this review because in so massive a tome anyone can find defects to suit his or her taste. There are gaps in the picture, such as the lack of any data on vertebrate predation or on the growth rates of trees. Certain figures are ambiguous or incomprehensible owing to lack of adequate captions or other deficiencies. In general, though, the editors can be praised for having done their job thoroughly. Altogether, this is an outstandingly fresh and significant work, with enough interest and scope to serve as a textbook. Most remarkably for a collection of papers, it contains a prodigious volume of new data. In the field of tropical ecology it is clearly a landmark and can be expected to stimulate comparative studies for many years to come.

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Reproductive Behavior

Mate Choice. PATRICK BATESON, Ed. Cambridge University Press, New York, 1983. xvi, 462 pp., illus. $59.50; paper, $19.95. Based on a conference, Cambridge, England, July 1981.

Charles Darwin brought to the attention of biologists mate choice, and particularly female choice of males, as a key element in understanding sexual pairing in animals. He and Wallace disagreed over the importance of female choice, and with the publication of *Mate Choice* it is apparent that this issue is not yet resolved. Ten of the 21 papers in this book focus on female choice in species in which males make no material contributions to females or their young. The ultimate basis for female choice in such mating systems has become one of the most controversial issues in evolutionary biology, and its emphasis in this book is timely and appropriate.

Females within polygynous populations often tend to show distinct preferences for a few males. It is commonly suggested that favored males are good sires. Current debate has centered on what evolutionary processes have shaped female mate choice. Authors in this book consider this and many other hypotheses.

Bradbury and Gibson present an insightful review of hypotheses concerned with the evolution of lek mating systems in birds and mammals. Leks deserve special attention because females are able to make mating decisions uninterrupted by male control and uninfluenced by material contributions made by males. Bradbury and Gibson evaluate factors affecting lek placement and favor the "hot spot" hypothesis over many other models including Bradbury's earlier home-range model. The causes of male aggregation and the basis for female choice are also considered. Bradbury and Gibson challenge the commonly held view that males preferred by females often hold central positions on leks and that females can use male position to judge the quality of prospective sires.

A much-needed description of recent models of runaway sexual selection is presented by Arnold. He endorses the runaway process as critical in explaining the extreme development of male display characters commonly seen in polygynous species. Arnold's valuable characterization is flawed by his suggestions that other good-genes models predict group-wide optimization of fitness and that males evolve maladaptive display characters. Recent sexual selection models are based on intersexual conflicts of interest that predict no such optimization. Display characters may lower male survival rates, but they evolve because they enhance individual male fitness. There is good reason to suspect that the runaway process may be important in sexual selection. However, the absence of any strong empirical support and the still primitive development of sexual selection theory suggest that Arnold's enthusiasm for the runaway process may not be justified.

O'Donald has been the most active modeler of the runaway process. His review of his earlier modeling efforts, a candid admission of a fundamental misunderstanding of the operation of runaway, and discussion of possible problems of polygenic models of sexual selection call attention to this paper.

Two wide-ranging reviews of mate choice are provided by Halliday and Partridge. Halliday embraces LeCroy's suggestion that females on leks don't really choose males. Bright plumes, common among polygynous birds, are said to evolve exclusively for male-male display. No convincing evidence is provided that supports this view, and Halliday fails to explain its major weakness: if female choice isn't the basis for lek formation, why do males group in leks and females find it necessary to attend these leks? Partridge reviews the rare male effect, effects of inbreeding and outbreeding, and the effect of polygynous mating on the loss of heritable genetic variation. She draws on a large body of literature in discussing each of these problems, but in most cases her conclusions are limited by the lack of appropriate data.

Parker suggests that much male display is associated with simple advertisement and that males better able to advertise will attract more mates. Thus, many male display characteristics commonly considered products of active female choice may be products of male advertisement. The economy of this approach makes it attractive because it circumvents many of the problems that arise when female choice operates. Such a model is useful for explaining long-distance female attraction to males but cannot explain female discrimination in favor of particular males once the female has moved within a male aggregation.

Arak is able to draw on a large number of studies of mate selection in anurans. He emphasizes the high cost of interspecific mismating and implies that frogs are especially susceptible to such errors. This may be due to the explosive breeding common in many species. The relatively sophisticated type of choice observed in species with long breeding seasons, such as bullfrogs, suggests that intraspecific discrimination may be important in some anurans.

Rowley's detailed review of re-mating in long-lived birds and Coulson and Thomas's summary of their work on kittiwake mating behavior deserve special attention.

The papers in this collection vary greatly in quality. Too frequently sentences appear that are uninterpretable, few new ideas are presented, and many topics that could have been covered are