valuable discussions of relevant chemical and biological topics. Some of his interpretations in these sections are unreasonably harsh, personal, and injudicious. The book is marred also by numerous minor errors of presentation and technical substance.

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Primate Socioecology

The St. Kitts Vervet. MICHAEL T. MCGUIRE and members of the Behavioral Sciences Foundation, University of California at Los Angeles. Karger, Basel, 1974. xii, 202 pp., illus. Paper, $20.50. Contributions to Primatology, vol. 1.

The relative accessibility of the large free-ranging population of vervet monkeys (*Cercopithecus aethiops*) on St. Kitts, introduced to the island over 300 years ago, provides unusually good opportunities for observation and experimentation. The main value of this book lies in the efforts of its authors to bridge the gap between the traditional qualitative descriptions of the behavior of free-ranging primates and the more sophisticated experimental techniques used in the study of laboratory animals. The admittedly limited success of their study in terms of results should be assessed against this background; the study may have a considerable influence on the direction of subsequent research.

The approach of the book is to describe the universe of possible behaviors for the vervet and to relate them to environmental variables through a summative reasoning equation (SRE). The starting point is a discussion of the ecology-influences-behavior and innate-repertoire hypotheses.

Food and water, range use, sleeping locations, and day plans are examined in terms of the SRE. Then there is a similar treatment of ranging behavior, group cohesion and dispersion, age and sex differences in behavior, play, grooming, hierarchy, sexual behavior, and group fission. The SRE is used to relate such conditions as population density, sources of disturbance, and birth and mating seasons to such behaviors as cohesion, coalitions, consort, aggression, play, and grooming.

The comparison of calls and gestures of vervets on St. Kitts and at Amboseli, which concentrates on variety (there is less on St. Kitts) rather than frequency, provides material for the subsequent discussion of elicited behavior and multiple social systems hypotheses and for a revision of the SRE.

Finally, the results are used in the discussion of some theoretical matters: population genetics of the vervet, including comparison between the island populations of St. Kitts and Lolui; the likely decreased genetic variability of the St. Kitts vervet; the concept of adaptation and its relevance to field studies; and the basis of socialization in terms of drive, sequential, reciprocal interaction, and drive consummation theories.

The authors bring refreshingly new ideas into the discussion of the behavior of free-ranging primates; these ideas may have an important part to play in the development of our understanding of, for example, the relations between environment and behavior. There is, however, a paucity of relevant data for the numerous hypotheses and formulas. Although the authors apparently recognize the complexity of relationships, such quantitative analyses as they provide are often insufficiently refined and detailed.

There is an emphasis on relatively crude measures of human and nonhuman disturbance and of population size and the tension of monkeys, but neglect of quantification of component behaviors in day plans, cohesion and dispersion, ranging patterns in relation to different biotic divisions within a group range (or territory), and the distribution therein of foods and feeding time. In the absence of such data the authors' conclusion that nutrients have no obvious effect on behavior can be of little value.

Qualitative data and involved theoretical discussion might have been portrayed graphically to greater effect, and the absence of photographs of monkeys and habitats is disappointing. So far there have been no experiments. The reader is told that there are important differences in behavior between the monkeys inhabiting forested ravines and those inhabiting the savanna-bush peninsula, but the nature, degree, and possible significance of these differences are not clear. The transposition of social groups from different biomes might help resolve the authors' speculations concerning the effects of habitat on behavior. There are several other instances of convoluted discussion, obscure conclusions, and arguments weakened by the lack of important evidence.

The authors' grasp of and ability to manipulate theoretical behavioral concepts are impressive. The theoretical framework they have built may be a major step forward in the quantitative description and interpretation of primate populations and social structure, yielding a fuller understanding of primate socioecology. The authors might, however, have paid more attention to recent advances in data collection and analysis in the field. Their perplexity on completion of their task is understandable; the problems facing primatologists are frustrating in their complexity, and solutions to many of them are possible only after detailed long-term studies. Continued efforts in the unusual situation on St. Kitts have clearly an important part to play in the resolution of these problems.

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Neotropical Biogeography

Avian Speciation in Tropical South America. With a Systematic Survey of the Toucans (Ramphastidae) and Jacamars (Galbulidae). JÜRGEN HAFFER. Nuttall Ornithological Club (% Museum of Comparative Zoology, Harvard University), Cambridge, Mass., 1974. viii, 390 pp., illus. $19. Publications of the Nuttall Ornithological Club, No. 14.

An airplane flight over tropical South America vividly confronts evolutionary biologists with a paradox. In the Amazonian rain forests below lives the most species-rich avifauna on earth. From horizon to horizon stretches the forest, homogeneous in appearance and, except for rivers, which can be circumvented at their headwaters, lacking in obvious barriers to bird dispersal. Yet the work of Mayr and others has shown that isolation of populations by geographic barriers is a prerequisite to speciation. Where are the barriers that permitted all those bird species to diverge?

For a long time the very richness of the neotropical fauna and flora and the size of South America kept neotropical biogeography in an information-gathering stage. Ecologists and evolutionary biologists who sought general principles were warned to turn their attention to the supposedly simpler and clearer problems of the temperate zones. Within

the past decade, however, progress has been made toward a synthesis of neotropical bird distributions that will be exciting to biologists in general. In the present book Jürgen Haffer, a leader in this emerging synthesis, summarizes present understanding of Pleistocene historical influences on neotropical bird speciation.

Haffer points out that Amazonia has not always been a dense, homogeneous green. During Pleistocene dry phases the rain forest survived in high-rainfall areas but was replaced by savanna and other open habitats in low-rainfall areas. As climate fluctuated (the fluctuations possibly, but not yet provenly, being correlated with glacial phases in the temperate zones), these forest "islands" alternately expanded and rejoined and contracted and became separate again, while opposite changes befell the savanna "islands." Haffer reasons that the temporary zones of alien habitat between these fluctuating habitat islands or refugia provided the dispersal barriers needed for speciation. Today, the ranges of neotropical forest bird species, semispecies, and subspecies are not randomly scattered over the map but are focused on a dozen or more major distributional centers. The substantial agreement between the location of these centers deduced from present bird distributions (Haffer's figure 13.1) and the location of the presumed forest refugia deduced from rainfall data (figure 5.7) supports Haffer's interpretation. Compressed within the book, as detailed supporting evidence, are valuable summaries of tropical South America's geological and climatic history; summaries of bird distribution patterns in the lowlands and Andes, emphasizing hybrid zones, zones of intergradation, and ranges of members of superspecies; and (occupying nearly half the book) a technical analysis of toucan and jacamar taxonomy and distributions, to illustrate the data base and the interpretations.

Two methodological problems affect details of Haffer's interpretations, and their solution will be crucial for further advances, though it is unlikely to undermine his basic concepts. First, Haffer deduces locations of distributional centers by a qualitative, intuitive approach (chapter 9): he surveys the data, detects repeated patterns, and lists the species exemplifying each pattern. An obstacle to a quantitative approach is simply the paucity of data available on neotropical bird distributions and relationships, as Haffer notes on p. 1. However, even present information might permit a more objective and quantitative, if crude, locating of distributional centers; for example, by superimposing a transect grid on a map of South America, determining the number of species range borders per unit distance, and identifying distributional centers from the contour lines through this map of border/distance values. Second, the book emphasizes historical factors relevant to dispersal and speciation, and in several instances (pp. 111, 160, 163) Haffer tacitly assumes that present conditions either fail to provide explanations or are to be invoked only as a last resort. Yet, even though savanna habitats as well as montane habitats are today disjunct, some bird species characteristic of these habitats may be able to colonize outlying habitat patches across the existing barriers, and fusions of patches or transient stepping stones may not have been required in the past in order for the birds to spread. Again, the homogeneous green of Amazonia conceals the facts that many forest bird species appear to be patchily distributed in this continuous habitat expanse, that these cases cannot all be dismissed as due to inadequate surveys, and that some cases may be due to the delicate, complex web of competitive relationships in the species-rich community itself. To what extent can we understand dispersal and isolation in terms of present conditions? Yes, historical factors are important in speciation, as Haffer has shown; but what is the relative importance of historical factors and of continuing processes?

For those who care not at all about tropical speciation or South American biogeography, this book will still be valuable in identifying ideal situations for studying numerous ecological and evolutionary problems. How are species-range borders in the middle of continuous forest stabilized (bottom of p. 107)? Where ranges of related semispecies abut without hybridization in continuous forest ("parapatry"), is competitive exclusion behavioral or based on resource preemption? Do some abutting relatives maintain interspecific territoriality, and in these cases do they converge in morphology, voice, or other territorial signals, as Martin Cody has postulated? Where distributions of related semispecies narrowly overlap, what are the niche shifts permitting local sympatry in the overlap zone? To what extent will refugia deduced from distributions of birds, butterflies, mammals, lizards, and plants coincide (pp. 150–157)? Can disjunct distributions of Amerindian stocks be similarly interpreted in terms of post-Pleistocene climate fluctuations, as Betty Meggers suggests? Do the differences in bird species diversity of South American and African rain forests have a historical explanation, such as that more refugia led to more speciation (p. 177)? Haffer's book will provide students with a treasure chest of research problems, until man's accelerating destruction of the richest habitat on earth blurs or obliterates not only the distributional patterns but also some of the species themselves.

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