

ROBERT W. SUSSMAN

PRIMATE ECOLOGY: PROBLEM-ORIENTED FIELD STUDIES



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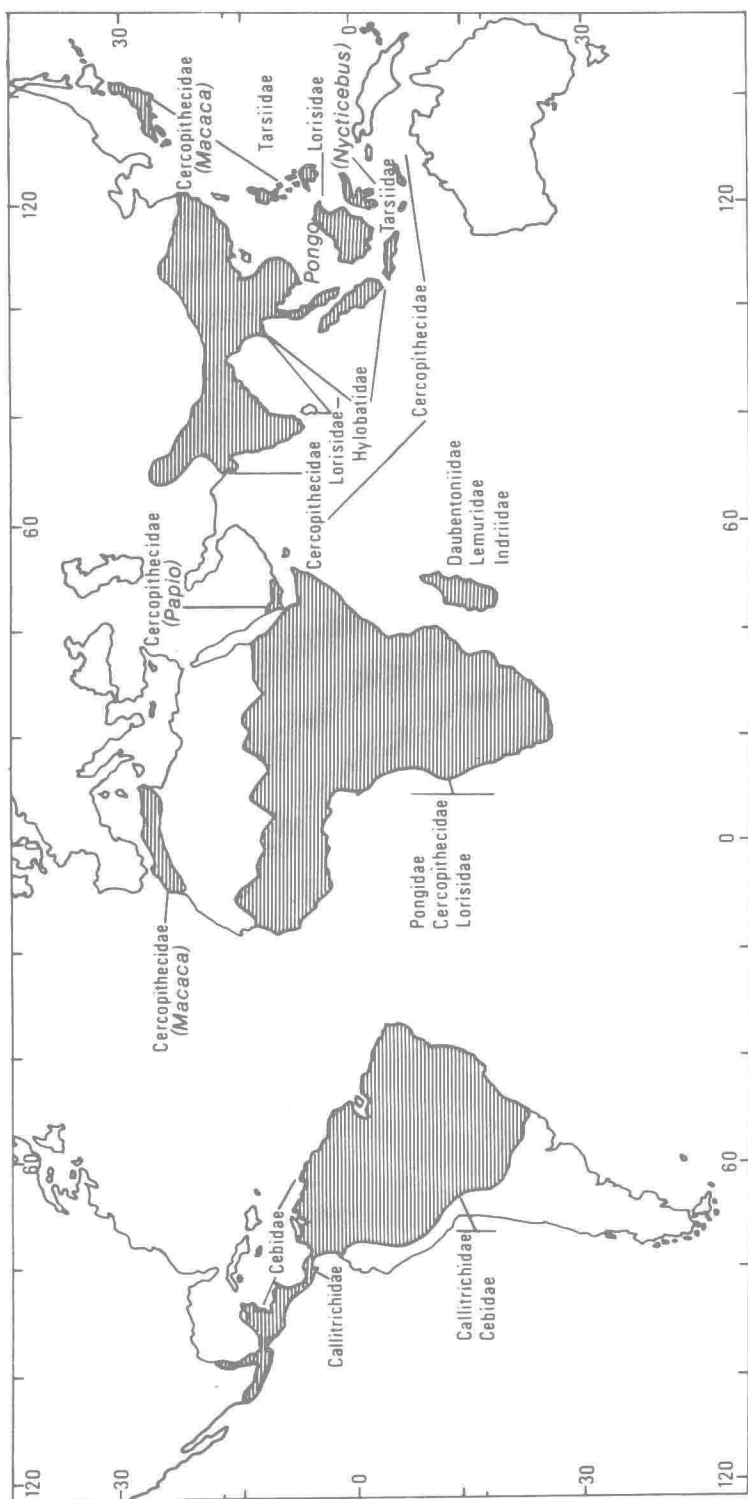
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PREFACE

Research on the ecology of naturally living primates has consisted of three major types of enquiry: general descriptive natural history; problem-oriented field research; and purely theoretical studies. Until recently most primate field studies have been of the first type. Natural history studies include detailed descriptions of the habits and habitats of the animals. This research provides us with basic knowledge of free-ranging primate populations, and is thus a necessary prerequisite for problem-oriented studies. Primatologists have collected data on a number of species living in their natural environment. However, for the most part, books presently available on primate behavior and ecology, either as textbooks or as readers, have concentrated solely on descriptive, natural history investigations, and usually on the most studied and easily accessible species.

An excellent brief history of field primatology up to the early 1960s can be found in Southwick (1963). Descriptive natural history of primates has continued up to the present but, as Southwick stated in 1963: "For most species of primates, our field knowledge is surprisingly sparse or non-existent" (p. 5). This is still true today, as will be discussed further in my introductory remarks to the various sections of this book.

Within the past 15 years the number of field investigations increased tremendously, and many primatologists have begun to do problem-oriented field studies. In these studies specific questions are posed. These questions are usually formulated either from general ecological theory or directly from data gathered during natural history research. Because of the problem orientation, the research is often, but not always, of shorter duration than that of more general natural history studies. It does not attempt to describe all aspects of the behavior of the species. This type of fieldwork is now becoming the most frequent and most important focus in primatology.

I consider the articles in this book to be a representative sample of this relatively new approach. These investigations are some of the earliest attempts at problem-oriented field research on primates. However, I have tried to choose articles that have somewhat similar themes and use relatively similar methods. In most of the articles, comparisons are made between certain aspects of the behavior and ecology of more than one species living in the same forest and utilizing potentially the same resources or between populations of one species living in different types of environment. In these studies, the investigator can relate specific habitat preferences to differences

in the morphology and social behavior of the species or populations under study. Because of the necessity of comparison, the fieldworkers have developed methods enabling them to quantify much of their data. These, however, are some of the first attempts at quantification of data collected in the field on habitat utilization by primates. I suspect that the techniques of data collection and the methods of analysis will improve rapidly. In fact, many studies now in progress and some already in press have become more sophisticated in both data collection and analysis. However, the articles in this book will stand as examples of the beginning of a new direction in primatology.

The book is divided into four initial sections arranged along systematic lines—prosimians, New World monkeys, Old World monkeys, and apes; a fifth section contains theoretical selections that deal with the question of relationships between social structure and ecology among primates. In organizing the first four sections I have used the following classification:

Order: Primates

Suborder: Prosimii (Prosimians)

Infraorder: Lemuriformes (lemurs)

Superfamily: Lemuroidea

Family: 1. Lemuridae
2. Indriidae

Superfamily: Daubentonioidea

Family: Daubentonioidea (aye aye)

Infraorder: Lorisiformes

Family: Lorisidae

Subfamily: 1. Lorisinae (lorises)
2. Galaginae (galagos)

Infraorder: Tarsiiformes (tarsiers)

Family: Tarsiidae

Suborder: Anthropoidea

Superfamily: Ceboidea (New World monkeys)

Family: 1. Cebidae
2. Callitrichidae

Superfamily: Cercopithecoidea (Old World monkeys)

Family: Cercopithecidae
Subfamily: Cercopithecinae
Colobinae

Superfamily: Hominoidea (apes and man)

Family: Hylobatidae (lesser apes)
Family: Pongidae (greater apes)
Family: Hominidae (man)

Although there are 16 selections in these four sections, because of the nature of the studies, certain aspects of the behavior and ecology of over 40 species of primate are presented.

The theoretical papers in the final section are presented in chronological order so that the reader can trace the stream of thought and the arguments as they are presented in the literature. These articles focus mainly on the following questions: What is the relationship between the environment or environments in which a species of primate is found and the social structure of that species? In other words, is there a relationship between ecology and social structure, and is this a necessary relationship? Given specific environmental conditions, how can a particular social structure increase the reproductive success of certain individuals? To what extent does genetic relationship (phylogeny) determine social structure regardless of environment? As will be seen as one reads the theoretical papers, although the questions remain the same, as more data are collected, the answers in many ways become more difficult to obtain. This is because we find that we need to make more subtle distinctions between the variables we are measuring. However, intensive, quantified, and comparative studies, such as those presented in this book, should allow us to collect the type of data needed to answer such questions and to formulate and test more sophisticated theories in primatology and in general ecology.

I would like to thank Pamela Ashmore and Robert Jamieson for their assistance in proofing and indexing the final manuscript and to dedicate this book to my parents, Louis and Helen Sussman.

Robert W. Sussman

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De Vore, I. (ed.). 1965. *Primate Behavior: Field Studies of Monkeys and Apes*. Holt, Rinehart and Winston, New York. (An early reader including natural history studies carried out in the late 1950s and early 1960s.)

Jay, P.C. (ed.). 1968. *Primates: Studies in Adaptation and Variability*. Holt, Rinehart and Winston, New York. (A reader dedicated to K.R.L. Hall, one of the first primatologists to do quantitative field studies on primates.)

Jolly, A. 1972. *The Evolution of Primate Behavior*. Macmillan, New York.

(A textbook and reference book on primate behavior. The relationships and distinctions between behavior in the field and in the laboratory are not always made clear. However, this is the first and best attempt to synthesize the extremely diverse literature in primatology.)

Kummer, H. 1971. *Primate Societies: Group Techniques of Ecological Adaptation*. Aldine, Chicago. (An excellent book on primate ecology that, however, concentrates on ground-dwelling forms.)

Napier, J.R. and P.H. Napier. 1967. *A Handbook of Living Primates*. Academic Press, London. (A catalog of the living primates, organized by genera.)

Southwick, C.H. 1963. *Primate Social Behavior*. Van Nostrand Reinhold, New York. (The first general reader concentrating on primate field studies. It contains a number of historically important papers.)

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PART 1

FIELD STUDIES

PROSIMIANS

introduction:

field studies on prosimians

Prosimians (the so-called “lower primates”) were the earliest primates to evolve, about 60 million years ago. They are often considered “primitive” in relation to the “more advanced” anthropoids (so-called “higher primates”), monkeys, apes, and humans. However, it must be kept in mind that the living prosimians are the end products of 60 million years of evolution. Although some may retain certain early primate features, many are very specialized, both morphologically and behaviorally.

As can be seen in the classification given in the Preface, the suborder Prosimii is divided into three major groups, or infraorders: Lorisiformes, Tarsiiformes, and Lemuriformes. Lorisiformes are represented by one family (Lorisidae) which, because of major differences in locomotor anatomy and behavior, is divided into two subfamilies: Lorisinae and Galaginae. All Lorisiformes are nocturnal (active at night and asleep during the day). The Lorisinae are slow-moving animals, two species of which are found in Asia and two in

tropical forests of Western Africa. Galagines are fast-moving animals, all six species of which are confined to Africa. Although a number of natural history studies have been done on the African forms of Lorisiformes, very little is known about the Asian lorises.

Selection I by Charles-Dominique describes a study of five species of lorises in a tropical evergreen forest in Gabon. This study began in 1965, and it is one of the longest continuous field studies on primates in their natural habitats. Charles-Dominique provides us with an excellent understanding of the variability in behavior and ecology found among nocturnal prosimians. He illustrates how, by selecting different habitats within the same forest, the five species avoid competing with one another for essential resources.

Tarsiiformes also have nocturnal activity cycles. Although there were a number of genera of tarsiers during the early evolution of primates (in the Eocene Epoch), there is only one living genus, *Tarsius*. The three living species are found in Southeast Asia on many islands of the Malay Archipelago. There is practically nothing known about naturally living populations of *Tarsius*. The only study now available (Fogden 1974) came about by accident when a number of tarsiers were trapped in mist-nets during a study of birds in Sarawak, Borneo.

The living Lemuriformes are all found on the islands of Madagascar and the Comoros. These primates have probably been isolated on Madagascar since the Eocene and have radiated into a number of diverse niches on this large island. In the present classificatory scheme there are three families (see preface) and 21 species. Among the Lemuriformes are the only diurnally active prosimians. In fact, approximately half of the species are diurnal. Detailed studies have been done on four of the diurnal species and one nocturnal species and preliminary studies on six others (see Richard and Sussman 1974 for references). Practically nothing is known about the natural behavior of 10 of the species.

The detailed studies of the Lorisiformes by Charles-Dominique, along with the studies of *Tarsius* (Fogden 1974) and the nocturnal lemuriform *Microcebus* (Martin 1974) indicate that these nocturnal prosimians share a generally similar social organization. In all of these forms, female ranges are small and overlap to a variable degree. Male ranges are usually larger and scarcely overlap with one another, although they overlap with one or more of the female ranges. This basic social pattern (referred to as "solitary but social" by Charles-Dominique) is found in a number of nocturnal mammals and may have been a primitive feature of the placental mammals.

As can be seen in the articles by myself and by Richard (Chapters 2 and 3), the diurnal lemurs have some behavioral and ecological adaptations that converge with those of anthropoids in a number of ways. Furthermore, all diurnal lemurs live in relatively permanent social groups, as do all anthropoids. The structure of these groups, however, is quite variable. This is true even within the same population for *Propithecus* (Selection 2). The study by Richard compares populations of *Propithecus* living in two vastly different environments. My study (Selection 3) of *Lemur catta* and *Lemur fulvus* compares these two species, both where they are sympatric and where they do not coexist. The three articles in this section illustrate three different methods utilized to quantify behavioral data collected in the fields.

Since the arrival of humans on Madagascar, approximately 2000 years ago, 14 species of lemur have become extinct. At present, all of the living species are gravely in danger of extinction. If conservation efforts are unsuccessful, we may never have the opportunity to learn more from these extremely unique and beautiful animals.

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