Book Reviews

Primate Socioecology

Reproductive Decisions. An Economic Analysis of Gelada Baboon Social Strategies. R. I. M. DUNBAR. Princeton University Press, Princeton, N.J., 1985. x, 266 pp., illus. $40; paper, $14.50. Monographs in Behavior and Ecology.

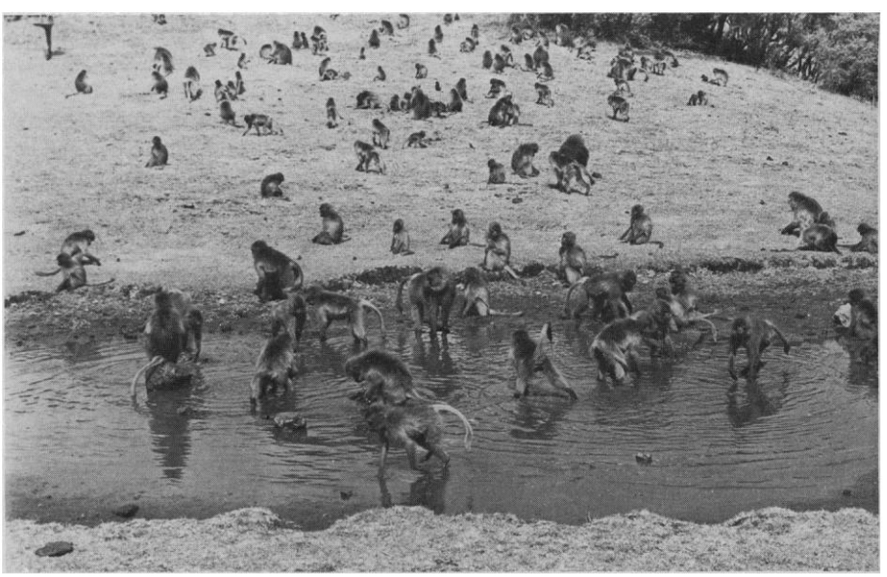
Gelada baboons, *Theropithecus gelada*, inhabit the spectacular highlands of the Ethiopian Amhara Plateau. Each day the geladas graze among the grasses of the plateaus, skillfully selecting grass blades or digging for grass roots; at night they roost upon the steep cliffs of the gorges that intersect the plateau. Adult males actively defend access to stable groups of mature females and their progeny. Most female gelada spend their lives in their natal units among their female kin and offspring, but males disperse as they mature, often joining all-male groups until they are able to take over or attach themselves to existing reproductive units. A number of discrete reproductive units and all-male groups, which occupy overlapping home ranges, constitute a band, and several bands may aggregate in herds of several hundred animals.

Much of this information about the gelada comes from the work of Robin and Patsy Dunbar, who observed free-ranging gelada in the early 1970's. In *Reproductive Decisions* Robin Dunbar integrates and extends earlier analyses of gelada socioecology. The central question in this book is: "Given that the gelada have the social system and ecological niche they do, how does an individual animal set about maximizing its personal reproductive output?" (p. 3). To answer this question, Dunbar documents the range of variation in behavior, demography, and reproductive performance observed among free-ranging male and female gelada and attempts to identify how proximate factors (such as climatic conditions and the socionomic sex ratio) produce this variation. In addition, he develops a number of mathematical models to evaluate the relative efficacy of these behavioral variants. The resulting body of work is one of the most complete analyses of the behavioral ecology of any primate species.

In the first three chapters Dunbar outlines the geladas' social organization, diet, ranging behavior, and activity patterns. Demographic processes and life history variables are considered in the fourth chapter. In chapters 5 and 6, Dunbar describes the formation of highly selective grooming relationships and alliances among females and considers the influence of these relationships upon the acquisition of dominance rank and female reproduction. Most of this material has been published previously. In the next three chapters, Dunbar ties these data together in a cogent analysis of female reproductive strategies and of the tactical options available to females to increase their reproductive success. Then he turns to male reproductive strategies, beginning with a discussion of how harem size and females' loyalties constrain males' ability to control access to them. In chapter 13 he details how some males join reproductive units as followers and other males take over units from resident males. In the next three chapters Dunbar develops a detailed model of male reproductive strategies, considering the range of options available to males and the relative advantages of each option under varying demographic and ecological conditions. The book concludes with a brief overview of the principal findings and a thoughtful discussion of the use of decision models in sociobiological studies.

In the analytical portions of the book, Dunbar integrates demographic information and behavioral data in models that provide plausible estimates of the costs and benefits of particular behavioral strategies. Then he uses these estimates to compare the relative advantages gained by individuals who adopt different behavioral strategies. This approach marks a significant departure in studies of primate social behavior. In most primate studies, costs and benefits cannot be measured in the appropriate biological currency of genes or offspring gained or lost; the variables in Hamilton's equation remain elusive abstractions.

Observations suggest that males pursue two distinct reproductive strategies. Some males attach themselves to large reproductive units and establish affiliative and sexual relationships with a small number of females within these units. After an initial rebuff, persistent followers are usually tolerated by resident males. Other males attempt to take over reproductive units and oust the resident male. Such attempts are usually resisted fiercely by the resident male, and males are sometimes wounded in these encounters. Dunbar found that followers acquired fewer females than males who successfully took over reproductive units, but followers joined units at younger ages, were more successful in their efforts to join units, and were less likely to be wounded in their initial attempts. Moreover, Dunbar finds that the size of the reproductive unit, the loyalty of females to their male, and the sex ratio in the population profoundly influence male behavior and confound simple predictions about the effect of alternative male strategies on male fitness. To deal with this complexity, Dunbar develops a dynamic model of male reproductive



"Part of a herd of gelada baboons." [From *Reproductive Decisions*]

strategies. After considerable effort, a simple conclusion emerges: the takeover and the follower strategies have approximately equal net payoffs to those who adopt them. Dunbar suggests that they are evolutionarily stable alternative reproductive strategies for males.

For females, dominance rank and the support of alliance partners are critical behavioral factors affecting fitness. Female gelada form linear dominance hierarchies, and a female's dominance rank is influenced by her age, her family's dominance rank, and the presence of an ally (usually her mother or daughter) who supports her in aggressive conflicts. Dunbar demonstrates that high-ranking females have higher birth rates than lower-ranking females and that females who receive support from an ally are likely to achieve higher rank than females who do not.

Dunbar addresses two related questions about females. First, how does coalition behavior evolve? Second, does fitness actually vary among females over the course of their lifetimes? His conclusions are likely to surprise many of his colleagues.

Dunbar's analysis of coalition behavior indicates that females principally benefit by increasing their personal fitness and gain relatively little through increases in their inclusive fitness. This result leads him to argue that coalition behavior has evolved primarily through individual selection, not through kin selection as many others have suggested. This conclusion rests upon several assumptions. First, alliances are assumed to impose no costs upon the participants, even though females expend time and energy in these encounters and are capable of seriously injuring one another with their canines; moreover, harassment by females apparently inhibits ovulation. Second, individual fitness is tabulated as the sum of benefits gained by a female and her daughters, whereas inclusive fitness is tabulated as the sum of benefits gained by her mother, sisters, and other female kin. These are not sensible classifications. Kin-selection theory provides no justification for distinguishing benefits gained through altruism toward mothers and daughters. If benefits gained through all kin are combined, the magnitude of the difference between the individual-selection and kin-selection components of fitness becomes considerably smaller. It is not clear how the results would be altered if the costs of coalition activities were incorporated into the model. Finally, it is evident that kinship is a critical ingredient of gelada alliances. Alliances typically involve closely related females, often mothers and daughters, and are only reciprocated over a period of many years. This is consistent with predictions from kin-selection theory and with Aoki's recent demonstration (*Proc. Natl. Acad. Sci. U.S.A.* **80**, 4065 [1983]) that kinship greatly facilitates the initial spread of alleles for reciprocal altruism. For these reasons, it seems clear that kin selection has played an important role in the evolution of alliances among gelada females.

Dunbar's analysis of female reproductive performance indicates that reproductive success is equilibrated among females over the course of their lifetimes. Though dominance rank influences reproductive performance in the short term, changes in rank that occur as females age tend to smooth out those differences. Dunbar cautions the reader that these conclusions do not necessarily apply to other gelada populations or other primate species. Such caution is warranted for several reasons. The gelada populations he studied were unusual in a number of ways. The population at Sankaber was expanding at an annual rate of 10.9 percent, food was abundant, infant survivorship was high, and predation was rare. Many of the demographic and behavioral data that were used in the analysis were collected during relatively short periods of observation. Estimates of infant and juvenile mortality, life expectancy, and female reproductive performance over the life span at Sankaber, for example, are based upon projections from cross-sectional data collected during two nine-month periods in the field. Dunbar's general conclusions will be accurate only if the behavioral and demographic patterns do not change over time.

These concerns do not diminish the value of Dunbar's work. Dunbar has presented the relevant data and outlined the assumptions of his models clearly, leaving the reader free to argue or agree with the conclusions he reaches. The models he builds can be used as a framework to explore a wide range of empirical circumstances and may some day become a useful foundation for broad comparative analyses. For those who wish to know more about geladas and for those who wish to consider cogent models of complex behavioral and demographic processes this book is essential.

JOAN B. SILK

Department of Anthropology,
Emory University,
Atlanta, Georgia 30322, and
California Primate Research Center,
University of California,
Davis 95616

Psychobiology

The Neurobiology of Motivation and Reward. JAMES R. STELLAR and ELIOT STELLAR. Springer-Verlag, New York, 1985. xii, 255 pp., illus. $34.90.

The study of motivation has been in serious decline for a number of years. The standard work in the field, by Bolles, is now 10 years old. Although individual systems such as thirst and hunger and the biology of reward processes have been the subjects of intense investigation, somehow more general issues relating to the theory of motivation have got left out. The rat is usually presented as a collection of bits rather than as a goal-directed organism. The theorists of the past addressed both motivation and learning, proposing models of their relatedness. Today's theorists are concerned primarily with learning. Unfortunately, in contemporary learning theory both the psychologist and the rat tend to get buried in ever more sophisticated and impressive cognitions, remote from motivation.

Given this general historical context, the appearance of *The Neurobiology of Motivation and Reward* by the father-and-son team of Eliot Stellar and James R. Stellar can only be described as an exciting event. Eliot Stellar is one of the pioneers of the subject.

The book's title suggests that it will be concerned primarily with the "hardware" end of the spectrum, and indeed it is. Much of the book is devoted to electrical brain stimulation, neuroanatomy, and neurochemistry. As a review of the neurobiology of the subject, the book is up-to-date, extensive, and well written.

The book is directed to a readership having some familiarity with psychobiology. It opens with a brief history of motivation and the concepts of reward, traced back to the Greeks. An introductory-level discussion relates these notions to instinct, hedonism, sensory psychology, temperament, emotion, and affect. This scene-setting is well done. However, the substance of the book concerns the hardware underlying reward processes. The rewarding effects of electrical stimulation of the brain are extensively discussed. The neurochemistry of reward and brain lesions also get extensive coverage. An overview at the end of the book is based mainly on the results of studies of electrical and chemical stimulation of the brain and of brain lesions. The coverage of these subjects is excellent. My regret is that the book does not return to the more general theoretical context of motivation, as is dis-