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Foreword

The stomach's empty: there it all begins.

—Bertoldt Brecht, *Three-Penny Opera*

How do individuals of various primate species fill their stomachs? What is the impact of differences in food resources on social structure, demography, ranging patterns, and daily activities? What biological and social processes are food-limited in the ecological sense of increasing when food availability increases? The answers to these questions require studies—within species, even within populations—that examine the effects of food when other factors such as taxonomic differences in morphology or physiology are not clouding the picture. Although the rich body of primate field studies that have accumulated during the past several decades have provided tidbits to suggest the profitability of such investigations, in this volume the topic is brought to center stage for the first time, with focus on one major source of food variability: food-enrichment that results from human activities.

The consequences of variability in food supply have often eluded quantitative investigation or clear interpretation. Situations of human-supplied food enrichment offer some unique research opportunities. Because the changes in food supply that result from direct, indirect, or inadvertent provisioning by humans are usually greater than those that result from foraging exclusively on wild foods, effects may be more easily discerned. In addition, changes in food availability that arise from human activities have direct implications for conservation and for coexistence of wildlife and humans because the resultant food enrichment will sometimes entail risks for the long-term survival of these animal populations. As wildlife areas experience more and more encroachment by human habitation, agricultural expansion, and tourism, studies of food-enhanced primates are significant not only for the insight they shed on basic biological questions but also for their potential contribution to urgent issues in conservation and wildlife management.

The immediately striking effects of food-enhancement are the dramatic changes in activity profiles, which are so well documented in this volume for

all the species and situations examined thus far. Whereas many of the initial findings have come from interpopulation comparisons, for which several factors may vary, a few within-population comparisons leave no question about the potency of food enrichment alone in producing a doubling of the time wild animals spent resting, halving of the time spent feeding, and smaller increases in the time spent socializing, as had been reported for animals in corrals or larger semi-captivity situations. This robust finding provides only a starting place, however. These effects raise major questions on every level of behavioral and population biology; and most of these have barely been elucidated, much less answered.

To what extent are changes in activity profiles of biological import in themselves? To what extent does time spent searching for and processing food constrain time available for other activities, and what are the consequences of such limitation? For example, Altmann [1980] suggested that increased foraging demands would result in less time available for socializing, whereas Dunbar [e.g., 1984] argued that maintaining social bonds is so important to group-living primates that socializing time is compromised only after resting time is used up. Recent studies reported in this volume and elsewhere [e.g., Lee et al., 1986; Saunders, 1987; Altmann and Muruthi, 1988] support an intermediate conclusion: socializing or grooming time do decrease with increasing foraging demands, though less so than does resting time, and social bonds are conserved with a reduced number of partners rather than time with each (or only one) being completely protected [Saunders, 1987]. These first results suggest the depth and subtlety of the investigations that will be both necessary and fruitful. It would not be at all surprising, for example, to find that the conservation of social bonds will differ across seasons, or across other conditions that differ in group stability or susceptibility to immigration or emigration, that effort toward maintenance of social relationships will differ by gender or age-class as a function of life-history variables for each species, and that the constraints within groups differ from those between groups.

To what extent do differences in allocation of time translate into differences in nutritional intake and energy expenditure? Most studies indicate that food-enriched groups spend the same or somewhat less time traveling than do totally wild-foraging groups. However, energy expended in travel is a function of the distance traveled, not the time spent traveling; differences in energy expended in travel may be much greater than suggested by time differences if food-enriched animals travel in a more leisurely fashion. That is the case among baboons in Amboseli, where there are no differences between a food-enriched group and wild-foraging ones in time spent walking, but a fourfold difference in distance traveled and a tenfold difference in annual home range size [e.g., Altmann and Muruthi, 1988; Muruthi, unpublished]. So, differences in energy expenditure are sometimes much greater than suggested by differences in activity profiles.

Translation of feeding time to nutritional intake is even more problematical than that for traveling time, and the relationship, even more than for traveling, probably is very different between groups, or even populations, than for comparisons between individuals within a single group. Do food-enriched animals take in less, the same, or more nutrients in their reduced time spent feeding? Judging by the very few data available thus far, the answer seems to depend on the nature of the enrichment conditions: crop-raiding, intentional feeding by managers or researchers, and scrounging of food at garbage dumps differ greatly in risks for the animals, as well as in quality and, to some extent, dispersal of food. From the few studies thus far reported, it is clear and should hardly come as a surprise, that the temporal and spatial distribution of food may be at least as important as the total quantity available.

Most situations of food enhancement are ones in which predictability of food availability is high and the spatial distribution of the food is very restricted. Many of the effects that we are coming to associate with high food availability may result from this clumping and predictability of food rather than its increased quantity. Social and demographic processes may be particularly susceptible to such spatial and temporal components of food enhancement.

Rates of aggression are greater at provisioning sites than elsewhere, but both observational and experimental studies suggest that the effects of differing levels of food availability are qualitatively different within high and low parts of the availability range. At relatively low levels of food availability, increasing food availability increases various forms of social behavior, whereas at high levels of well-dispersed provisioning, competition sometimes decreases [e.g., Southwick, 1967; Belzung and Anderson, 1986; Lee, 1984 and this volume]. Food availability and predictability have effects on parent-offspring interaction as well, both indirectly, through demographic changes, and directly, as reviewed by Berman and by Rosenblum (this volume).

The effects of food availability cannot be considered independent of effects on demographic processes. Although we can be confident that food enhancement will reduce age of first reproduction, rates of infant mortality, and length of interbirth intervals, the effects on adult mortality are more ambiguous, and the effects on the various life history stages are probably not quantitatively the same, even for those animals in which the qualitative effects are similar. Moreover, it is here that the importance of considering the within-group variability in effect rather than just the group mean is highlighted. For example, the data on Japanese macaques, as summarized by several authors in this volume and originally reported by Mori [1979], Sugiyama and Ohsawa [1982], and others, suggest that reproductive parameters such as age of first reproduction exhibit greater variability among individuals, greater differentiation by social rank, when there is provisioning than when there is not. The existence, and generality, of this finding, have considerable implications for the genetic and other aspects of population processes and for social processes that

are a function of social and genetic structure within groups (e.g., reviewed by Berman this volume). Development of population models such as those outlined by Lyles and Dobson in this volume and those by Cohen [e.g., 1972] and others earlier, will be an integral part of future work. However, application of such models to real populations and to management issues will depend on incorporating features that detect and are sensitive to fluctuations and recent changes in demographic parameters, not just equilibrium conditions. A large stochastic component and changing conditions have probably always been a major feature of primate life at the level of the individual and the group, but this situation is surely exaggerated in the situations involving human-nonhuman primate interactions that we encounter today.

Some of the best documented effects of food enhancement are those of developmental acceleration, resulting in shorter prereproductive stages. However, we know little or nothing about parallel effects on other parameters during development. Are all aspects of physical development promoted equally? The data for Japanese macaques suggest that skeletal development is less accelerated than is rate of growth in body mass, for example. And what of development in social and other behaviors? Do these accelerate at similar rates? If not, what are the consequences of changed co-occurrences among developmental stages? For example, in Amboseli baboons, wild-foraging females usually attain their place in the dominance hierarchy about a year before reproductive maturation. If under conditions of enrichment reproductive maturation is accelerated by at least a year but social maturation is not comparably advanced, females may be faced with the turmoil of social rank changes at the same time they meet the challenge of caring for their first infant. This provides just one example of the potential costs of apparently advantageous effects of food enrichment when there may be different sensitivities to food enrichment or a negative correlation among relevant reproductive or life-history parameters. These, in addition to ecological factors such as disease transmission discussed by Lyles and Dobson (this volume) among others, may put considerable constraints on the extent to which food is a limiting factor in primate population processes and may indicate that population changes would, in such cases, be made only with concomitant major changes in social structure and behavior.

The topics addressed in the present volume are ones of major import for the study of behavior and population processes in both human and nonhuman primates. Food enrichment is a complex, non-unitary phenomenon, at one end of a continuum of resource variability. Where food enrichment cannot or should not be eliminated, its thorough investigation may ultimately be one of the most illuminating in primate behavioral biology.

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