

Foraging for Survival: Yearling Baboons in Africa. By STUART A. ALTMANN. Chicago: Univ. of Chicago Press, 1998. Pp. 608. \$70.

One of the premier primatologists, in this book Stuart Altmann summarizes his thoughts after conducting fascinating research on baboons in Amboseli National Park for many decades. Altmann sets forth three goals for the book: to provide (1) a behaviorist's and natural historian's description of an intriguing ecosystem and how young baboons cope with this environment, especially through their foraging behavior; (2) a conceptualization of a young baboon's foraging behavior, using a mathematical model that defines optimal foraging decisions and comparing model predictions with observed foraging choices; and (3) an explanation of how baboon foraging may serve as a model system for assessing the foraging decisions of the primate ancestors of humans. Natural historians, animal behaviorists, ecologists, and anthropologists should prize all three goals, and Altmann provides much information on these topics.

However, this is a somewhat difficult work to read, because the three goals are not balanced or well integrated. First, the book is exhaustive (372 pages of text, 54 pages of appendices, and 121 pages of tables), focusing on data collected over a single year (1974–1975) on 11 yearling baboons in a single social unit. Second, for those more concerned with natural history, behavior, and anthropology, the book may present less of interest (approximately 140 pages) than to those interested in optimal foraging models and their application. Third, throughout the work, Altmann provides us with many points that diverge from the work's main focus. These distract the reader from the principal story and often are little more than personal opinion. However, personal opinions may be interesting when they come from a primatologist of Altmann's renown.

The majority of the book focuses on the development of mathematical models for optimal foraging decisions, their parameterization, and comparison of predicted to observed diets for yearling baboons. The models are based on the well-established optimization technique of linear programming. The description of their application to yearling baboons is covered in the minutest detail, and 10 different models based on five potential foraging goals and different sets of foraging constraints emerge. While models with the goal of energy maximization (greatest energy intake per day, given constraints to food intake such as mineral needs, protein requirements, digestive capacity, water intake, etc.) bear resemblance to the observed diets of yearling baboons, there are marked discrepancies. For example, the best fit between the average predicted and observed diets is only 38 percent, and for individual diets the best fit was only 17 to 63 percent. Altmann argues that the predicted optimal diet is a benchmark that few if any individuals can attain, and therefore poor performance should be expected.

Given my own interest in foraging models, I was astonished by the extremely poor fit between predicted and observed diets, given the generally good fit of these types of models (averaging 85 percent in over 400 studies [1]). The explanation for this lack of fit in Altmann's study may be very simple, and he even briefly admits to this likelihood in Chapter 6, saying that the digestive capacity and feeding time constraints are not realistically calculated. The digestive capacity does not incorporate realistic turnover rates of foods through the baboon's digestive tract, and the feeding time constraint does not incorporate the search time

for food and movement between feeding patches (Appendix 1). Both lead to overestimates of potential food intake. Therefore, there is very good reason to question the appropriateness of the optimal foraging models' structure and parameters. Rather than being convinced of the models' utility, I was left with more questions—such as whether maternal foraging and social rank might strongly influence yearling foraging—and I wondered why Altmann did not pay more attention to these issues.

Altmann's foraging models, the centerpiece of this book, also suffer from not taking advantage of the existing foraging literature. While Altmann and Wagner provided an early call for the employment of linear programming to the study of optimal foraging [2], the application of optimal foraging theory in this book is not up-to-date. First, it seems that the review of optimal foraging literature largely ends in 1986. For example, Altmann argues that rate-maximizing foraging (greatest nutrient intake per unit of foraging time) is the mainstay of the field, but practitioners in the field have long known that rate maximization only applies if foods are randomly or uniformly distributed in the environment [3]. In addition, Altmann argues that his progress on applying linear programming to his baboons (most data collected from 1974–1975) was retarded by the need to develop a rate-maximizing linear program model (Appendix 6). However, this has already been done, and it was shown that the predictions of linear programming and classic rate-maximizing optimal foraging models are identical if foods are randomly or uniformly distributed [4]. Second, Altmann refers to computational obstacles. How can this be, when most PC-based spreadsheets (Excel, Quatro, Lotus, etc.) include linear-programming capabilities, a mainstay of business planning? Third, Altmann falls into the trap of testing his models' predictions against diet predictions that have an element of circularity. The observed diets (mass/day) are computed as the product of observed time spent feeding on each food (min/day) and the food's harvesting rate (mass/min). However, the harvesting rate is part of the models' feeding time constraint. Therefore, the models should be used to predict time spent feeding on each food (min/day) and compared with this observed value to avoid circularity. These and many other problems have been addressed in the optimal foraging literature.

Altmann argues that his optimal foraging models, even with all their faults, serve as benchmarks against which an individual's actual foraging can be compared, and that deviations should be correlated with individual differences in future survival and reproduction. Indeed, these deviations *are* highly correlated with future survival and reproduction (correlations greater than 90 percent). This is a tantalizing result and supports the assumption that foraging decisions are related to an individual's fitness. Altmann is correct to claim that foraging models serve as benchmarks to standardize individual foraging performance against potential performance, as the individual changes in foraging ability and needs with ontogeny and as the availability of foods change seasonally. However, one must question the value of these correlations when the optimal foraging models perform so poorly in predicting observed diets, and when they appear to be constructed by ignoring major elements of the time and digestive capacity constraints. Again, Altmann misses a thorough study of this issue using linear programming models of foraging with ground squirrels [5–7]. In Ritchie's work, the linear programming model predicts actual foraging very well (81 to 94 percent of the variance); survival and repro-

duction throughout life are demonstrated to be correlated with deviation from the predicted optimal diet; and an individual's foraging performance is correlated with its mother's foraging performance (inherited ability) and improves through life (learning)—all with much larger sample sizes.

Altmann's book contains a wealth of information on baboon foraging and nutrition that can be used in optimal foraging models that are more complete than developed in the book. These data are invaluable to primatologists interested in foraging, as are Altmann's thoughts on primate foraging and its evolution. Furthermore, I would recommend this book to anyone initiating a research program in optimal foraging, because Altmann lays out all of the considerations that practitioners in this field follow, but do not have the luxury to include in much more concise journal articles.

REFERENCES

1. Belovsky. *Oecologia* 100:175–80, 1994.
2. Altmann and Wagner. *Recent Adv. Primatol.* 1:407–14, 1978.
3. Stephens and Krebs. *Foraging Theory*. Princeton: Princeton Univ. Press, 1986.
4. Belovsky, et al. *J. Theor. Population Biol.* 36:144–60, 1989.
5. Ritchie. *Evol. Ecol.* 2:232–52, 1988.
6. Ritchie. *Oecologia* 82:56–67, 1990.
7. Ritchie. *Evol. Ecol.* 5:146–59, 1991.

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Guns, Germs, and Steel: The Fates of Human Societies. By JARED DIAMOND. New York: Norton, 1999. Pp. 480. \$14.95 (paperback).*

Originally published in 1997, this remarkable, Pulitzer Prize-winning book has just been reissued in paperback. Since its initial publication, it has received much well-deserved praise for its singular insights and the breadth of its scholarship, as well as for its graceful style. In time, it will undoubtedly take its rightful place among the classics of history, perhaps at the head of the classics, since it describes the foundations of human civilization, the history of pre-history, if such an oxymoron is permitted.

Every historian brings to his task certain assets, such as knowledge of language and culture, and access to museums or libraries. The pre-historian must have an entirely different set of assets: scientific knowledge of evolution, ecology, anthropology, archeology, and mainly curiosity. Diamond has all of these in abundance.

* *Editor's Note.*—From time to time, we miss a book that should have been reviewed and that remains a most valuable source of information for our readers. Diamond's is such a book.—M. F. Arnsdorf.