THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(29 October - 16 November 1990)

"The Population Dynamics and Conservation of Primate Populations"

Andrew P. DOBSON
Princeton University
Department of Ecology
and Evolutionary Biology
Princeton, NJ 08544
U.S.A.

The Population Dynamics and Conservation of Primate Populations

ANDREW P. DOBSON
Department of Biology
University of Rochester
Rochester, NY 14627, U.S.A.*

ANNA MARIE LYLES
Department of Biology
Princeton University
Princeton, NJ 08544, U.S.A.
and
New York Zoological Society
Bronx, NY 10460, U.S.A.

Abstract: *Primates are among the most threatened taxa, with more than half of all species in jeopardy. In this paper we develop population models to use the kind of data on wild primates that primatologists actually collect. Our survey of recent primate journals suggests that the average field study uses 1.5 years of data from 50 animals. The models are based on the simple Leslie-Lefkovitch matrix. They suggest a simple method that allows assessment, from a few years' data, of whether a population is collapsing and requires intervention. To a good approximation, populations will collapse when adult survival, per inter-birth interval, is less than 70 percent.*

Modifications of the basic model incorporate more realistic assumptions about social organization and density-dependent resource limitation. These allow us to identify population densities at which potential Allee effects operate, and permit more precise estimates of the minimum population sizes and compositions required for successful reintroductions to the wild. The most important result is that populations of primates that live in small family groups may be more prone to "demographic" extinction than are more promiscuous species that live in more extended groups.

Resumen: *Los primates están entre los taxa mas amenazados, con más de la mitad de todas las especies en peligro. En este informe desarrollamos modelos de poblaciones para utilizar el tipo de datos que los primatólogos recopilan sobre primates en estado silvestre. Nuestra revisión de revistas recientes sobre primatología, sugiere que un estudio de campo, en promedio, utiliza 1.5 años de datos sobre 50 animales. Los modelos están basados en la matriz simple de Leslie-Lefkovitch. Estos sugieren un metodo simple que permite evaluar con datos de solo algunos años si una población está colapsando y, por lo tanto, requiere de intervención. Una buena approximación sostendría que las poblaciones colapsan cuando la sobrevivencia de la población adulta en los intérvalos entre nacimientos es menor al 70%.*

Las modificaciones del modelo básico incorporan premisas más realistas sobre la organización social y las limitantes de recursos que dependen de la densidad. Esto nos permite identificar densidades de poblaciones en las que potencialmente operan efectos de Allee y estimar más precisamente el tamaño mínimo de población y la composición poblacional requeridos para una reintroducción existosa a la vida silvestre.

El resultado más importante es que las poblaciones de primates que viven en pequeños grupos familiares son más propensas a la extinción "demográfica," que aquellas especies más promiscuas que viven en grupos más grandes.

362

Introduction

Conservation biologists are attempting to preserve the 227 extant species of primates through a range of approaches (Benirschke 1986). Most populations of non-human primates number 300 to 100,000, making their total populations smaller than most small human cities or towns (Jolly 1985; Mittermeier 1986). Although governments have set aside reserves where whole communities of primates may be preserved, land development and exploitation continue to encroach upon the remaining regions of primate habitat. Additional pressure on primate populations comes from hunting and from live-capture for captive colonies and research (Diamond 1985; Mittermeier et al. 1986; Wolfheim 1983). Researchers can monitor only a handful of these threatened communities, and furthermore, they can only study a few of each community's species in depth (Bourliere 1985; Terborgh 1983; Waser 1987). At the most endangered level of this spectrum, captive breeding programs maintain genetic diversity (Jones 1986; Western 1986); it is hoped that these programs will save some species for eventual reintroduction to the wild (Lyles & May 1987; May & Lyles 1987; Kleiman 1989).

In a 1975 report, the United States National Research Council officially recognized the alarming declines in primate populations. The report called for increased study of primate population dynamics to identify factors that affect a habitat's carrying capacity and to develop management guidelines for sustained harvesting of populations. The report did stimulate more collection of information on primate population dynamics, but lack of standardization made comparative analyses difficult. The 1981 publication, *Techniques for the Study of Primate Population Ecology* (National Research Council) provides a better basis for studying primate demography. Now, although the need for primate population management is recognized (Johnson & Whitehair 1986), few other quantitative guidelines exist.

Determining a population's status with only limited demographic data looms as the urgent problem facing many conservation-minded primatologists (Southwick et al. 1986). Our goal is to design some relatively simple models that reveal as much as possible about primate population dynamics from limited amounts of available data. Our hope is that such models can allow useful insights into factors that determine the ability of endangered populations to persist.

We begin with a literature survey to show the type of data commonly collected in primate field studies. We then develop some simple population models where we assume that mortality and fecundity are independent of a hypothetical primate's population size. We then add mathematical functions to mimic the affects of social organization on reproductive success. These models ex-amine the dynamics of primate populations in the absence of resource limitations (e.g., populations that are recently introduced into a new habitat, those that are unnaturally small because of poaching, or those that are extensively provisioned in parks, large zoos, or artificial colonies). The model is next adjusted for populations where resource requirements, predation, or disease act in some way to regulate population growth. These models are more appropriate for less disturbed, free-living populations of primates. In both cases a broad array of behavioral mechanisms are condensed into a few simple mathematical functions. In each section we have attempted to keep the amount of mathematics to a minimum and have depicted all significant results graphically.

Survey of Primatological Field Studies

To determine the type of data normally collected in current primate field work, a survey of the recent literature was undertaken. The survey covers the 234 papers with field observations of natural primate populations published during the five years 1981 through 1985. It encompasses the four major primatology journals: the *American Journal of Primatology*, *Folia Primatologia*, the *International Journal of Primatology*, and *Primates* (additional details are presented in Appendix 1).

Roughly one quarter (16–34 percent) of the articles in these journals were devoted to field studies. Of these, about a tenth are field surveys or community or comparative studies with data from multiple genera. However, most studies (79 percent) concentrate upon single populations of one species. Nearly half (45 percent) of the research takes place in Africa and Madagascar, with Asia and the Neotropics claiming respectively 31 percent and 24 percent of the papers. The geographical origin of publications has become more equitable than it was from 1931 to 1981 (Southwick & Smith 1986). The survey includes 55 percent of the extant primate genera, although 58 percent of the papers are devoted to only four genera: *Alouatta*, *Macaca*, *Papio*, and *Pan*. As illustrated in Figure 1, most papers focus upon behavior, while information on ecology or populations (particularly those aspects relevant to behavioral ecology) is often given as well.

Ideally, demographic data should be compiled from large numbers of known individuals that are observed for many generations. In reality, the mean number of subjects is around 50, though the range, from 1 to 7,000, is large! Primates are individually identified in half the studies, and data are usually provided for several social groups. Thus, while the number of study animals is smaller than one might wish, the quality of data for these individuals is usually very good. Unfortunately, the duration of studies tends to fall short of even one generation: the median length of observation was only 1.5
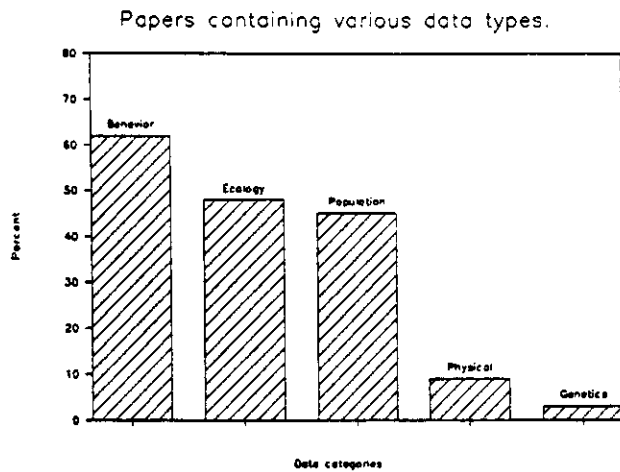
Papers containing various data types.

Figure 1. *Percentage of papers published in the primate literature (1981–85) containing data pertaining to each of five different categories of primate research. (Appendix 1 gives a full definition for each category.)*

years. In general, most primate field studies last for about as long as it takes to satisfy doctoral research requirements.

The tendency for cooperative study of single populations (46 percent of studies) mitigates the short-duration problem to some extent. If the individual studies occur sequentially, cooperative research makes possible the collection of long-term demographic information. Collaborators, unlike independent researchers, tend to recognize individual subjects (X^2 = 66.0, d.f. = 1, p < 0.001). A collaborator's paper more often has a behavioral focus than does an independent researcher's (X^2 = 4.8, d.f. = 1, p = 0.03). The collaborator's data also tend to cover longer time spans (mean = 3.2 versus 1.6 years: Figure 2). Longer studies more often include data on populations and ecology (X^2 = 8.7 and 10.1, respectively, d.f. = 1, p < 0.01), and these data are for greater numbers of animals (X^2 = 4.9, d.f. = 1, p = 0.03). Excepting some unusually productive independent research, cooperative projects tend to produce more demographic data. Unfortunately, publication of this long-term information is erratic: cooperative projects produced from 0 to 14 papers per year, with an average of 2.8 annually.

To supplement our five-year survey, we collected additional estimates of basic demographic rates from primate populations studies (Table 1). Good estimates are often available for fecundity, and useful data are sometimes available for adult survival. One frustrating feature of the table, however, is the absence of parameter estimates for which data must be available. *The importance of publishing this data cannot be overemphasized;* complete sets of demographic data are only available for 9 of the 50 populations.
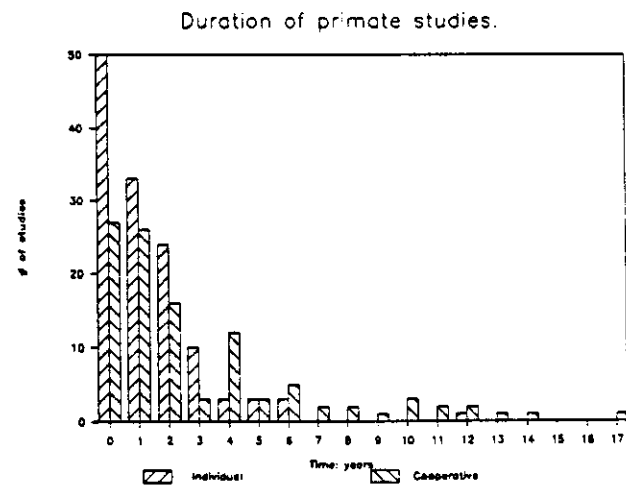
Duration of primate studies.

Figure 2. *Frequency distribution of duration of primate studies. The vertical axis gives the number of studies; the horizontal axis gives the duration of the study in years. In each case the column to the left of the hash mark gives data for studies undertaken by individuals and the data to the right gives data for cooperative studies.*

The review confirms that demographic interests per se provide limited motivation for primate studies. Extrapolating from the 2 percent of the American Society of Primatologist's membership who claim ecological specialization (Dukelow 1983), probably only a small fraction of primate researchers are trained to use ecological methods. Furthermore, few primate field researchers live in countries with wild primates (Terry 1983).

Simple Models of Primate Population Dynamics

Our survey suggests that models for primate populations must find ways to accommodate data from relatively small studies of short duration. Under these circumstances, management decisions must be based on crude estimates of demographic parameters supplemented with extrapolations from related species. We therefore adopt an approach to primate demography that assumes that only limited time or facilities are available to ascertain basic demographic parameters. Instead of attempting to develop a species-specific life table analysis, we develop a general model based upon the Leslie matrix (Leslie 1945, 1948). Models of this type usually require age-dependent estimates of survival and fecundity. They have previously been applied to several specific primate populations (e.g., Altmann et al. 1985; Rawlins & Kessler 1988). However, when data are limited, large errors are likely to be present in estimates of survival and fecundity for animals at different ages. Repeated multiplication of these estimates in fully age-

Table 1. Primate life history data.

Species and study site	Feeding level	Type of pop.	Study years	Number studied	Age at first reprod	Birth rate (/yr)	Surv. to age 1	Surv. to 1st reprod	Annual adult mort	References
Alouatta palliata										
B.C.I., Panama	0	N	1973–77	≈56	≈4	0.48	≈0.6	≈0.37	≈0.18	Froehlich et al. 1981
Guanacaste, Costa Rica	0	N/D	1970–78	>33	3.5	0.53	0.59	—	0.03	Glander 1980
Ateles geoffroyi										
B.C.I., Panama	0	I	1975–80	12	≈6.5	0.38	—	—	—	Milton 1981
Cebuella pygmaea										
Maniti, Peru	0	N	1976–77	2–9	—	1.70 (twin)	0.67 (6 mths)	—	—	Soini 1982
Cercopithecus aethiops										
Amboseli, Kenya	0	N	1977–80	11–28	—	0.73	0.40	—	—	Cheney et al. 1981
North Senegal	0	N	1975–76	33–47	—	≈0.50	0.65	—	0.15	Galat & Galat-Luong 1977
Samburu/Isiolo, Kenya	0	N	1977–80	37–40	—	0.58	0.59	—	—	Whitten 1983
Lolui Island, Uganda	1	D	1963–64	—	—	0.83	—	—	—	Gartlan 1969
St. Kitts, West Indies	1	I/D	1971–73	4–65	—	0.83	—	—	—	McGuire 1974
Barbados, West Indies	1	I	1979–83	12–19	≈4	1.20	≈0.7	≈0.5	—	Horrocks 1986
Sepulveda, California, U.S.A.	4	I/A	1975–83	14–23	4.1	1.00	0.90	0.90	—	Fairbanks & McGuire 1984
Cercopithecus mitus										
Kibale, Uganda	0	N	1977–80	11–24	—	0.21	0.90 (6 mths)	—	—	Butynski 1982
Macaca fasicularis										
Ketambe, Sumatra	0	N	1980–84	—	—	0.65	0.80	—	—	van Schaik & van Noordwijk 1985
Macaca fuscata										
Mt. Kawaradake, Japan	0	N	1972–74	100	—	0.52	0.64	—	—	Ikeda 1982
Mt. Kuniwari, Japan	0	N	1975–79	13–47	—	0.44	0.74	0.70	0.12	Maruhashi 1982
Shiga Heights B, Japan	0	N	—	—	—	0.35	0.53	—	—	Suzuki et al. 1975
Mt. Ryozen, Japan	0	N	1974–80	20–60	6.7	0.34	0.73	0.57	0.026	Sugiyama & Ohsawa 1982
Koshima Islet, Japan	1	N	1952–63	20–50	5.3	0.46	0.96	—	0.039	Mori 1979
Koshima Islet, Japan	1	N	1972–77	≈105	6.8	0.32	0.31	—	0.081	Mori 1979
Shiga Heights A, Japan	2–4	N	1962–75	—	—	0.51	0.86	—	—	Suzuki et al. 1975
Mt. Ryozen, Japan	3	N	1969–73	45–80	5.2	0.59	0.82	0.72	0.008	Sugiyama & Ohsawa 1982
Ohirayama, Japan	3	I	1957–69	—	—	0.58	0.76 (6 mths)	—	—	Tanaka et al. 1970
Koshima Islet, Japan	3	N	1964–71	50–120	6.2	0.67	0.85	—	0.021	Mori 1979
Laredo, Texas, U.S.A.	3	I	1974–79	130–222	5.9	0.18	0.93	0.64	≈0.09	Fedigan et al. 1983; Gouzoules et al. 1982
Arishiyama A, Japan	3–4	N	1954–74	34–158	5–6	0.73	0.90	—	—	Koyama 1980; Koyama et al. 1975
Arishiyama B, Japan	3–4	N	1975–77	210–270	—	.53–.68	—	—	—	Takahata 1980
Takasakiyama, Japan	3–4	N	1950–75	—	5	0.63	0.89	—	—	Itani 1975; Ohsawa et al. 1977
Rome Zoo, Italy	4	I	1977–81	27–51	—	0.86	—	—	—	Scucchi 1984
Macaca mulatta										
Dunga Gali, Pakistan	0	N	1978–79	≈290	—	0.38	0.55	—	—	Melnick 1981 (in Richard 1985)
Aligarh District, India	1	N	1959–77	0–36	—	0.77	0.82	≈0.08	0.17	Southwick et al. 1980
Chhatari, Aligarh, India	1–2	N	1959–77	8–132	—	0.90	0.84	≈0.30	0.09	Southwick et al. 1980
Kathmandu, Nepal	2	N	1975–78	292–358	—	0.62	0.78	0.41	0.22	Teas et al. 1981
LaParguera, Puerto Rico	3	I	1962–72	106–364	4.0	0.73	0.83	0.63	—	Drickamer 1974
Cayo Santiago, P.R., U.S.A.	3–4	I/D	1959–62	30–130	≈4	0.80	0.92	—	0.065	Koford 1965
Cayo Santiago, P.R., U.S.A.	3–4	I	1976–83	59–306	≈4	0.80	0.93	≈0.80	0.068	Rawlins et al. 1984
Tuglagabad, India	4	N	1980–83	28–133	—	0.82	>0.96	0.96	—	Malik et al. 1984
CPRC, Davis, U.S.A.	4	A	1977–79	—	3–4	—	0.81	0.71	—	Smith 1982
Yerkes, Georgia, U.S.A.	4	A	1972–77	—	3.8	0.84	—	—	—	Wilson et al. 1978
Macaca sinica										
Polonnaruwa, Sri Lanka	0–1	N	1968–72	8–43	≈5	0.69	≈0.47	0.15	≈0.004	Dittus 1975, 1977
Anuradhapura, Sri Lanka	0–1	N/D	1968–71	—	—	0.69	0.64	—	0.11	Dittus 1975
Macaca sylvanus										
Ain Kahla, Morocco	0	N	1968–69	14–39	—	≈0.5	—	—	—	Deag 1984
Algeria	0	N	1983–84	16–44	5	0.2–1.0	0.17–1.0	—	—	Menard et al. 1985
Gibraltar	4	I	1936–80	20–30	4.7	0.49	0.93	0.90	0.011	Fa 1984
Salem, FRG	4	I	1977–83	81–178	4.8	≈0.5	0.92	—	—	Paul & Thommen 1984
Papio anubis										
Gilgil, Kenya	0	D	1971–81	48–100	5.8–7.7	.43–.71	—	—	0.05–.2	Strum & Western 1982
Papio cynocephalus										
Amboseli, Kenya	0	N	1963–83	28–79	≈6	0.55	0.47	—	0.1–.15	Altmann et al. 1977, 1981, 1985

4

Table 1.   Continued.

Species and study site	Feeding level	Type of pop.	Study years	Number studied	Age at first reprod	Birth rate (/yr)	Surv. to age 1	Surv. to 1st reprod	Annual adult mort.	References
Papio hamadryas										
Erer, Ethiopia	0	N	1971–77	61–69	6.1	≈0.5	0.82	0.64	—	Sigg et al. 1982
Presbytis entellus										
Kanha, India	0	N	1980–83	≈30	—	0.75	—	—	—	Newton 1986
Dharwar, India	1–2	D	1961–63	17	—	0.86	—	—	—	Sugiyama 1965
Abu, India	≈2	D	1971–74	14–24	—	0.27	—	—	—	Hrdy 1977
Jodhpur, India	2–3	D	1967–82	8–82	3.4	0.85	0.62	—	—	Winkler et al. 1984
Theropithecus gelada										
Gich, Ethiopia	0	N	1973–74	16–112	—	.15–.40	0.82 (6 mths)	—	0.06	Ohsawa 1979
Sankaber, Ethiopia	0	N	1971–74	85–289	4–4.5	0.37	≈0.96	≈0.88	—	Dunbar 1980
Gorilla gorilla										
Virunga, Rwanda/Zaire	0	D	1972–75	12	10.1	0.36	≈0.60	—	—	Harcourt et al. 1981
Pan troglodytes										
Bossou, Guinea	0	N	1976–83	19–21	—	0.23	—	—	—	Sugiyama 1984
Gombe, Tanzania	2–3	N	1965–83	31–60	14	0.19	0.73	0.59	0.08	Goodall 1983
Mahale, Tanzania	2–3	N	1965–83	≈100	13	0.13	0.63	—	—	Haraiwa-Hasegawa et al. 1984
Pongo pygmaeus										
Tanjung Puting, Borneo	—	N	1971–75	58	15	≈0.2	≈0.91	—	—	Galdikas 1981

These data were collected from the published literature on 53 primate populations. The data and abbreviations used in each column are:

Feeding level: 0 = no artificial provisioning; 1 = occasional light provisioning; 2 = regular, light provisioning; 3 = regular, heavy provisioning; 4 = entirely dependent upon artificial provisioning. The data for different populations of the same species are ordered by increasing provisioning rate.

Type of population: N = natural, D = disturbed, I = introduced, A = artificial.

Study years: when the population was studied.

Number studied: total number of individual animals in the study population during the course of the study.

Age at first reproduction: in years.

Birth rate: average number of offspring born per female per year.

Survival to age one: proportion of offspring that live to age one (in four cases data is only available to age 6 months).

Survival to first reproduction: proportion of offspring that survive to begin breeding.

Annual adult mortality: proportion of adult population dying each year.

structured models is likely to lead to uncontrolled error propagation. Therefore, models for species conservation need to balance the number of parameters required to characterize a population against the data available to estimate those parameters.

Here we avoid the complexities of a fully age-structured model by noting that for most primate species, age at first reproduction is approximately three times the average interbirth interval (Fig. 3, Lyles & Dobson 1988). However, group-living primate species tend to have slightly earlier ages at first reproduction than monogamous ones, and captive populations may have earlier ages at first reproduction than free-living ones (Lyles & Dobson 1988). Nevertheless, this useful approximation allows construction of a more managable *stage*-structured model (rather than *age*-structured) called a Lefkovitch matrix (Lefkovitch 1965). The population is coarsely divided into three stage classes: infants, *I*; immatures, *J*; and adults, *A*; with time normalized into "inter-birth interval" units. The effects of changes in individual life-history parameters for a wide range of primate species may thus be systematically compared within a common framework. When age at first reproduction, *a*, is two inter-birth intervals, the basic model can be written as:

$$\begin{bmatrix} I \\ J \\ A \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & Ff(N_t) \\ si & 0 & 0 \\ 0 & s & s \end{bmatrix} \cdot \begin{bmatrix} I \\ J \\ A \end{bmatrix}_t \quad (1)$$

Here s equals the survival of an immature or adult through one inter-birth interval time unit, i is the relative density-independent survival of an infant through its first inter-birth interval, and F equals the maximum female fecundity through one time unit. In this model, our primary concern is the female portion of the population. The function relating fecundity to population density, $f(N_t)$, allows examination of the dynamic consequences of different types of social organization or resource use; this will be discussed in the next section. Initially we assume that all females find mates and that postadolescent survival is constant. Let us also assume that adult females can always produce one offspring during each inter-birth interval, and thus a daughter every two intervals. Though simple, these initial assumptions capture the essential features of primate demography.

First we concentrate on one key demographic variable, λ, the intrinsic rate of increase of the population, essentially the rate at which the population size changes during the course of one interval. If λ is greater than
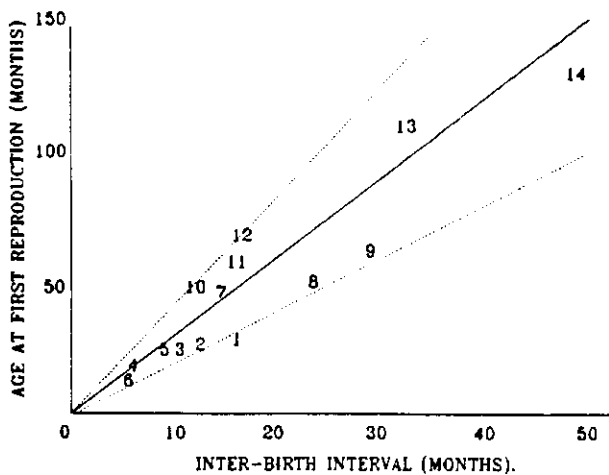
Figure 3. *The relationship between age at first repro-duction and inter-birth interval for primates. The data are taken from Harvey & Clutton-Brock (1985), and are given as means for each subfamily (less than 10 percent of the variation in these parameters occurs at lower taxonomic levels). The numbers cor-respond to each of the following subfamilies: (1) Lemurinae, (2) Lorisinae, (3) Galignae, (4) Tarsidae, (5) Callitrichidae, (6) Callimiconidae, (7) Cebinae, (8) Alouattinae, (9) Atelinae, (10) Aotinae, (11) Cercopithecinae, (12) Colobinae, (13) Hylobatidae, and (14) Pongidae. The solid line has slope three, the upper dashed line has slope four, and the lower dashed line has slope two.*

unity, populations increase; if λ is less than unity, pop-ulations decline and will eventually go extinct. In the absence of any density dependence (i.e., $f(Nt) = 1$), λ is given by solving the expression

$$\lambda^a = \frac{s^a\, i\, F}{\lambda - s} \tag{2}$$

Thus the population will only be able to maintain itself when

$$s^a\, i\, F > 1 - s \tag{3}$$

Adult and infant survival rates that result in λ greater than unity are depicted in Figure 4 for three different relative ages at first reproduction. Populations with *i* and *s* that give values of λ greater than unity will grow, or will be constrained at some carrying capacity by re-source limitation. Populations with values of λ less than unity will decline to eventual extinction.

Nine populations from Table 1 have sufficient data to estimate *i* and *s*. These estimates are superimposed on the isoclines of Figure 4; long-term population trends for four of these populations are illustrated in Figure 5. These data confirm the utility of this simple approach by illustrating that stable and growing populations of pri-mates have values of λ greater than unity (Figs. 5a, c, and d), while declining populations may be identified by
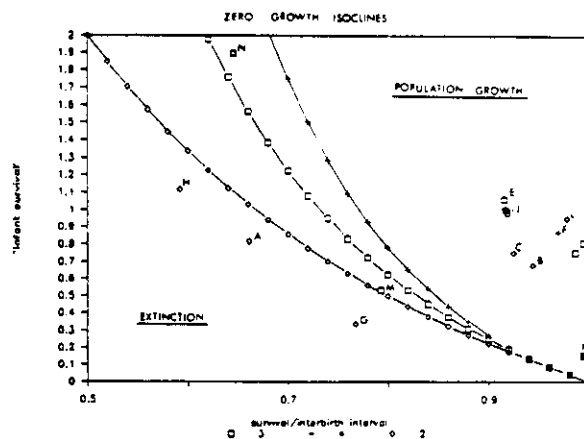

Figure 4. *Diagram of values of* i *and* s *that give rise to either increasing or declining populations. The isocline for* λ = 1 *separates populations that tend to increase (above the line) from those that tend to col-lapse; lines are drawn for three relative ages for first reproduction: 2, 3, and 4 inter-birth intervals. Data for nine populations from the survey in Table 1 are superimposed upon the diagram (the symbol for each species corresponds to its appropriate age at first reproduction). The data used are (a) Allouatta palliata on Barro Colorado Island, Panama (Froeh-lich et al. 1981). (b) A. palliata at Guanacaste, Costa Rica (Glander 1980). (c and d) Macaca fuscata at My Ryozen, Japan (Sugiyama & Ohsawa 1982b); the data for (d) are from a period when the population was artificially provisioned (e, f, and g) M. fuscata at Koshima Islet, Japan (Mori 1979); (e) were lightly provisioned, (f) heavily provisioned, and (g) received no provisioning. (h) M. fuscata at Laredo, Texas (Fedigan et al. 1983), a previously provisioned troop transported and left to "relearn" its foraging skills. (i,j) Provisioned M. mulatta on Cayo Santiago, Puerto Rico; (i) 1959–62, Koford (1965), (j) 1976–83, Raw-lins et al. (1984). (k) M. sinica at Polonnaruwa, Sri Lanka (Dittus 1975, 1977). (l) M. sylvanus at Gibraltar (Fa 1984). (m) Papio cynocephalus at Am-boseli, Kenya (Altmann et al. 1977, 1981, 1985). (n) Pan troglodytes at Gombe, Tanzania (Goodall 1983).*

low values of *i* and *s* (Fig. 5b). In particular, the Japanese macaques transferred to Laredo, Texas (Fedigan et al. 1983), and the baboons in Amboseli, Kenya (Altmann et al. 1985), have values of λ less than unity. The data from the Japanese macaques at Koshima Islet (Mori 1979) are particularly informative since this population exhibited a period of slow growth when lightly provisioned, a period of rapid growth following increased provision-ing, and a decline when artificial provisioning ceased (Fig. 5a). Appropriate changes in the estimates of λ are obtained for the different periods of study (Figs. 4e, f, and g).

6

A.

Macaques at Koshima

B.

Baboons in Amboseli.

C.

Gombe Chimpanzees

D.

Cayo Santiago Macaques
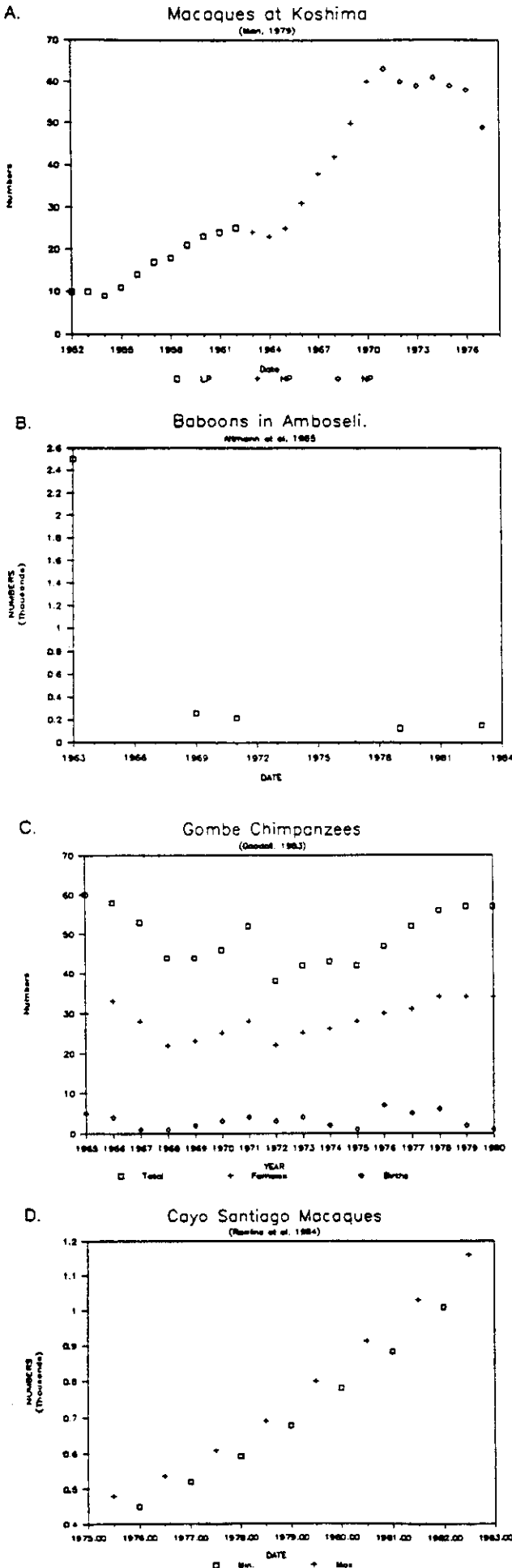
Social Structure and Allee Effects

Social organization in primates varies from monogamous pairs to large promiscuous groups (Smuts et al. 1987). Ultimately, interactions between the social system and the distribution of resources and predators determine social organization (Jolly 1985; Terborgh & Janson 1986; Wrangham 1980, 1987). These interactions influence rates of birth, death, immigration, and emigration, which in turn produce group-size frequency distributions indicative of the underlying social system (Cohen 1969, 1971, 1972). Data from several long-term studies suggest that these distributions are either Poisson or negative binomial in form (Fig. 6). We also note that habitat fragmentation will tend to break populations into groups of different sizes. We assume that fragmentation's dynamic consequences for group size may be modeled by one of these frequency distributions.

Behavioral ecologists customarily assume that females in estrus will be inseminated. The probability that pregnancy will result depends on a variety of physiological variables; we assume that these remain constant in mature females. When modeling populations that may be threatened with collapse, it is worth reconsidering the assumption that all females are mated. The ability of females to find mates is likely to depend both on population density (Allee 1931) and on the degree of subdivision of the population into either social or "habitat fragment" groups. Assuming negligible female-female interference in mate-finding at low population densities, the probability of insemination depends on the duration of female receptivity, the social group's size, the number of males in each group, and male promiscuity.

We can examine mating probabilities by using functions originally derived for parasitic helminths (May 1977), and by using frequency distributions of group sizes to characterize key demographic aspects of primate social organization and habitat fragmentation. The functions give the probability of a female being inseminated, $f_i(N)$, for either of the two distributions. In the Poisson case, which corresponds to primates living in groups of random size, the expression is of the form

$$f_1(N) = \left[1 - \left[_e - (N/T)(pm/(1 + m))\right]\right]^{\Gamma} \quad (4)$$

Figure 5. Observed patterns of population density for four primate populations. (A) (e, f, and g in Fig. 4) M. fuscata at Koshima Islet, Japan (Mori 1979); (lp) lightly provisioned, (hp) heavily provisioned, (np) artificial provisioning ceased. (B) (m in Fig. 4) Papio cynocephalus at Amboseli, Kenya (Altmann et al. 1985). (C) (n in Fig. 4) Pan troglodytes at Gombe, Tanzania (Goodall 1983). (D) (i and j in Fig. 4) Provisioned M. mulatta on Cayo Santiago, Puerto Rico (data from Rawlins et al. 1984).
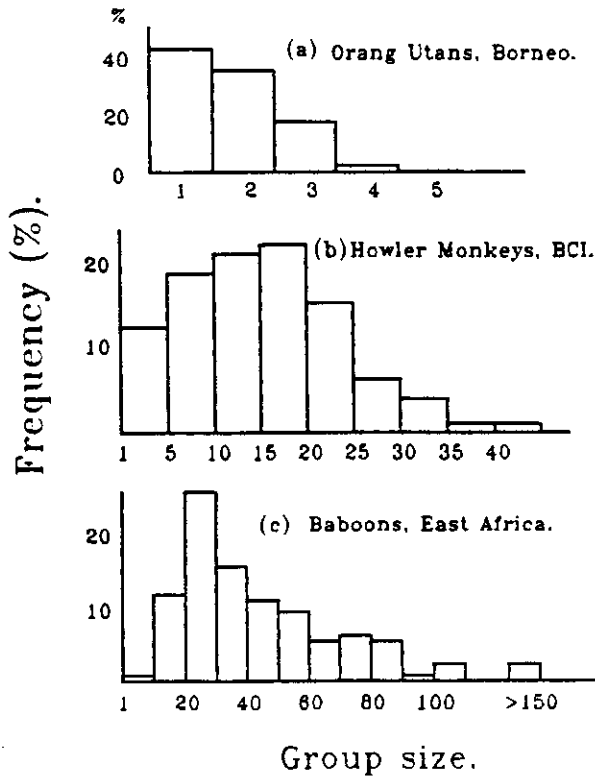
Group size.

Figure 6. Frequency distributions of group sizes in wild primate populations. The data in (a) are for orang-utans in Borneo, from Mackinnon (1974) in Cohen (1975). The data in (b) are for howler monkeys on Barro Colorado Island, from Carpenter (1962). The data in (c) are mixed data for two species of baboons in East Africa (see Cohen 1969). The top frequency distribution conforms to a Poisson, while the lower two are truncated negative binomial distributions (see Cohen 1969).

Here N is the total number of females in the population, T is the number of troops (or fragments) they are divided into, m is the number of males per female in the population (the sex ratio), p is the average number of females each male mates with (an index of promiscuity), and Γ is a phenomenological parameter that may be coarsely considered as an index of the length of time it takes for mates to associate with each other before successfully consorting; larger values of Γ lead to reductions in the frequency of successful matings.

A similar function may be derived for the case where troop size is distributed as a negative binomial (May 1977):

$$f_2(N) = \left[1 - [1 + (N/Tk)(pm/(1 + m))]^{-1-k}\right]^{\Gamma} \quad (5)$$

Here k is a parameter of the negative binomial distribution that varies indirectly with the degree of aggregation of the individuals into troops of different sizes. The other parameters are as in Table 2. The influence of

Table 2.   Parameters used in the models described in this paper.

s	= survival of adult females per inter-birth interval.
I	= scaling parameter for survival of infant primates; the product sI gives infant survival during the first inter-birth interval of life.
F	= number of female offspring produced by a female in one inter-birth interval; here assumed to equal 1/2.
a	= age at first reproduction in inter-birth time intervals.
λ	= the rate of increase of the population per inter-birth interval.
T	= the number of troops a population is divided into.
m	= the adult sex ratio, expressed as number of males per female.
p	= the average number of females each male mates with.
Γ	= an index of the length of time it takes for mates to consort with each other.
k	= a parameter of the negative binomial distribution that inversely characterizes the degree of aggregation of individuals in troops.
b	= a parameter of the density-dependent function that determines how closely offspring production is linked to available resources.
K	= a parameter of the density-dependent function that determines the level of available resources.

social organizations on mating probability is illustrated in Figure 7. Although the probability of insemination always increases with population size, females of species characterized by variability in group sizes have much higher chances of mating at low population densities than do females of species characterized by more equitable group sizes, though the latter do better at higher population densities.

The functions that coarsely represent different extremes of social organization (equations 4 and 5) may
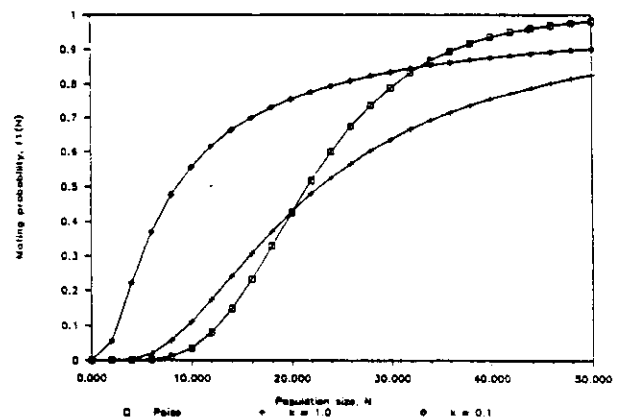

Figure 7. The influence of different characteristic frequency distributions of group size on the probability that a female locates a potential mate. The lowest line (□) depicts the case for a Poisson distribution of group sizes, the intermediate curve (+) is for a partially aggregated distribution (k = 1.0), and the top line (◊) indicates the case for a highly aggregated distribution, k = 0.1. In all cases the population is assumed to be divided into four troops (T = 4), with p = 1.0, m = 1.0, and Γ = 10.

be substituted into equation 1. An expression for the threshold population density, N_T* the numbers of individuals required to establish a reintroduced population, may then be obtained by solving this expression at equilibrium (Appendix 2). Populations that exceed this threshold will grow, those that are less than it will decline to extinction. For the Poisson case the threshold is given by

$$N_T^* = \frac{T(1 + m)}{pm} \ln\left[\frac{1}{1 - \left[\frac{1 - s}{s^2 \, iF}\right]^{1/\Gamma}}\right] \quad (6)$$

While for the negative binomial case, the threshold occurs at

$$N_T^* = \frac{T(1 + m)k}{pm}\left[\left[\frac{1}{\left[1 - \left[\frac{1 - s}{s^2 \, iF}\right]^{1/\Gamma}\right]}\right]^{(1/1 + k)} - 1\right] \quad (7)$$

We first note that because $f(N_t)$ can only reduce fecundity, the ability of the population to persist still requires that the inequality in equation 3 be met ($\lambda > 1$). This result is independent of the function used to mimic an Allee effect. The influence of the other parameters on threshold population size are depicted in Figure 8.

These results suggest a new and important insight into the management of primate populations: *Species that tend to live in aggregated groups with promiscuous mating will establish and maintain themselves at smaller population densities than species with more solitary and monogamous habits.* Social organization is thus a crucial consideration in determining the population densities required for reintroductions, and in determining the threshold densities below which endangered populations are likely to collapse.

Density-dependent Resource Limitation and Primate Demography

In wild primate populations, some form of resource limitation must ultimately set a population's upper level of abundance (Dittus 1977, 1979, 1980; Dunbar 1987; Lyles & Dobson 1988; Strum & Western 1982). Differential allocation of food resources according to social dominance, both within and between groups, determines the physical condition and hence the survival and fertility of different females (Dunbar 1987; Fedigan 1983; Silk 1987; van Schaik 1983; Waser & Starling 1986; Wrangham 1987). In hard years only occupants of the richest ranges may be able to reproduce. At low population densities only the best habitats might be used; as population density increases, ranges will expand into lower quality territories, perhaps leading to decreased fecundity. Similarly, while membership in a
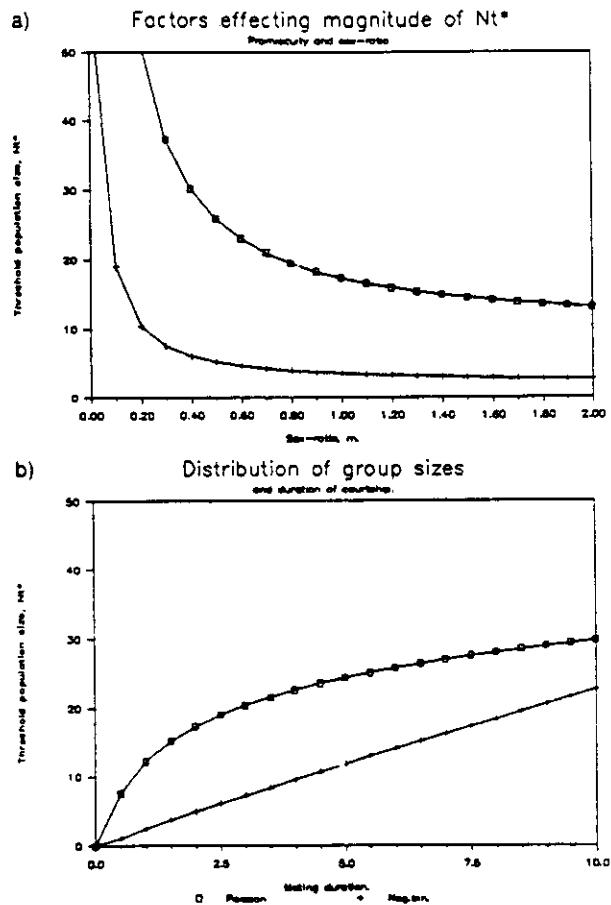
a)   Factors effecting magnitude of Nt*

b)   Distribution of group sizes

Figure 8. (a) The influence of variations in the sex ratio on the threshold population density, N_T^*, below which the population collapses. The curves are drawn for Poisson group sizes with sex ratio expressed as males per female. Thresholds are illustrated for two values of p (the level of promiscuity); the upper case illustrates the relationship when p = 1 (=monogamous), the lower for p = 5 (promiscuous). In both cases the time taken for mates to consort is relatively short (Γ = 2). (b) This figure illustrates the influence of average duration of mating activity, Γ, on the threshold population density. The lower curve is for primates aggregated in four troops with k = 0.5; the upper case is for a Poisson distribution of troop sizes. In both figures s = i = 0.8 and F = 0.5.

large group may afford better access to resources or protection from predators, it may also be energetically costly because of intra-group competition (Janson & van Schaik 1988; van Schaik 1983; Wrangham 1980). In seasonal environments, resource limitation may only operate periodically, usually during the dry season when animals are obliged to use "keystone plant resources" (Terborgh 1986). Thus, at very high population density, group ranges may contract and rates of encounters between individual group members may in-

crease. In turn, this may lead to increases in aggression and even in mortality (Cheney 1987). Dittus (1977, 1979) has hypothesized that aggression and affiliated behaviors ultimately mediate density-dependent regulation in primates.

Although a variety of subtle behavioral mechanisms influence the relationship between population density, mean fecundity, and social organization, we make no attempt to discuss their relative merits. Instead, the salient features of the regulatory mechanisms will be captured by a population-level model. Here we ignore the effect of mating system (i.e., equations 4 and 5) and assume that the probability of each female producing an infant in a troop of size N is now given by the function

$$f_2(N) = 1/[1 + (N/K)^b] \qquad (8)$$

This function was originally described by Sheperd (1982); it is a modification of one that Fowler (1981) suggested is sensible for large mammal populations. Two parameters determine the relationship between fecundity and population density (Fig. 9). One of these, b, determines how fecundity is linked to per capita resource abundance; the other, K, varies with resource abundance. When b is greater than unity, birth becomes highly dependent upon the carrying capacity of the environment; when b is less than unity, the fecundity is less closely linked to population density. The former case corresponds to tight linkage of social interactions with availability of food or other limiting resources, while the latter corresponds to looser linkage. Essentially we assume that increasing resources will lead to greater carrying capacities. This will mean that the social mechanisms that influence fecundity will come into play at higher population densities.

We can again include the density-dependent function into our basic matrix framework (equation 1), but now allow the birth rate of female infants to depend on the total number of adults and immatures in the population. Analytical details of the model's properties are given in Appendix 2; here we present the more translucent results. Total equilibrium population density is now given by the expression

$$N^* = K \left[\frac{s^a \, iF}{(1 - s)} - 1 \right]^{(1/b)} \qquad (9)$$

Thus population size varies directly with the level of resource abundance K and inversely with the strength of the recruitment parameter b. Simple proportionality gives the numbers in each subsection of the population, with sN^* adults, $(1 - s)N^*$ immatures, and $[(1 - s)/si]N^*$ infants in the population during any interval. In most cases, increases in survival lead to increases in the total population size and in the ratio of adults to immature animals. Increased fecundity leads only to increases
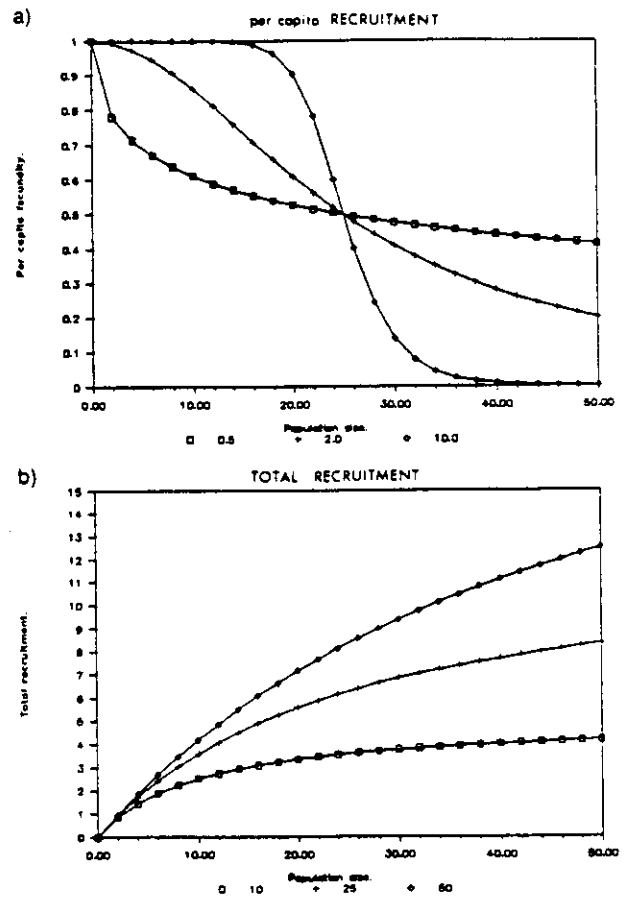

Figure 9. Relationship between population density and fecundity for characteristic values of the density-dependent function (equation 8). The upper figure, (a), illustrates the influence of the strength of regulation on the relationship between per capita fecundity and population size. The figure is drawn for three values of b (0.5, 2.0, and 10) with K = 25. The lower figure, (b), illustrates the influence of available resources, K, on the relationship between population size and total births in the population. This figure is drawn for three values of K (10, 25, and 50) with regulation strength or intensity held constant at b = 1.

in the total population density; age structure does not change.

The dynamic behavior of the population may be explored using local stability analysis (Beddington 1974). This exercise suggests that four patterns of population dynamics may be observed in primate populations (Fig. 10). Where recruitment is only loosely coupled to population density (b is relatively low), populations tend to return asymptomatically to equilibrium when perturbed. As the strength of regulation increases, perturbations cause damped oscillations that die out as the population returns to its carrying capacity. Very strong regulation potentially produces stable limit cycles and more complex dynamic variations in the population

/ O

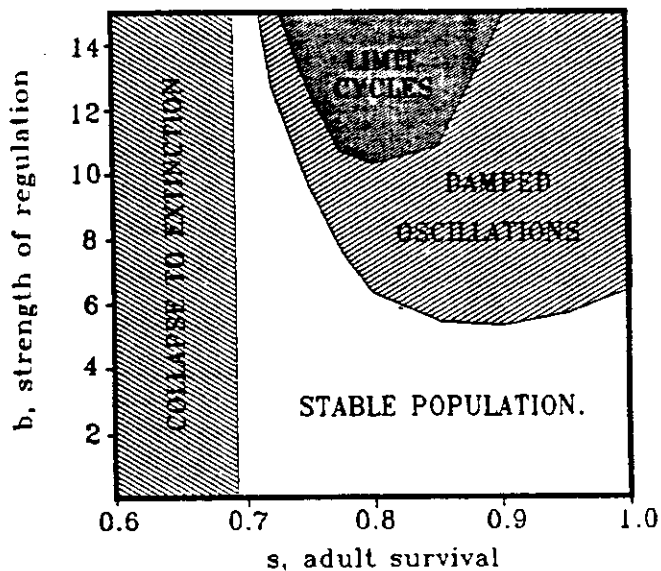## DYNAMIC BEHAVIOR OF BASIC PRIMATE MODEL.

Figure 10. The dynamic behavior of the model for different values of b *and* s *(the figure is drawn for* i = 0.75). *Populations to the right of the line where* s ~ 0.7 *will persist, while those to the left of this line collapse to extinction. In the region of persistence, the populations either return to a stable density when perturbed, or exhibit damped or limit cycles of abundance. The positions of the boundaries delineating regions of different dynamic behavior are independent of the magnitude of* K.

size. An important conservation "rule of thumb" emerges for cases with *i* and *F* close to unity: *Populations collapse when the survival of adult females falls below around 70 percent per inter-birth interval.* This value corresponds to λ falling below unity, as in equation 2. The result is completely independent of the form of the density-dependent function. It further emphasizes the importance of estimating survival per inter-birth interval when assessing primate population viability.

The model's different dynamic patterns are illustrated in Figure 11 for several sets of parameter values. These figures illustrate that primate populations respond to perturbations on a time scale of several inter-birth intervals and thus *many years.* In particular, the populations in Figures 11a and 11b take 20 to 30 inter-birth intervals to either grow to carrying capacity or collapse to extinction. Very few primate studies even approach these time scales. The simulation in Figure 11d illustrates the consequences of habitat loss on a hypothetical primate population. Here it is important to notice that the normal regulatory function (equation 8) causes a very rapid decline in birth rates (i.e., number of infants) following habitat loss; declines in adult numbers follow more slowly. These simulated disruptions are likely to underestimate declines in wild primate populations

where habitat loss may also lead to increased adult mortality and fragmentation of the population.

Models with Both Allee Effects and Resource Limitation

The density-dependent function (equation 9) may be combined with the mating function (equations 4 and 5) to produce a model that considers both the availability of mates and resource limitation. This is done by simply inserting both functions into equation 1. A graphical analysis of the full model's behavior is illustrated in Figure 12. Persistence of any population is again conditional upon satisfying the inequality of equation 3; however, the population's growth is also determined by its density. Provided that density exceeds a lower threshold, the population will increase to an upper density where intraspecific competition for resources or other forms of density dependence determine abundance. However, populations near or below the "threshold for establishment" will tend to collapse to extinction. The magnitude of this lower equilibrium is determined largely by intrinsic factors, such as social organization, sex ratio, and duration of pair bonds. In contrast, extrinsic factors such as habitat destruction and reductions in survival and fecundity are more important in determining decreases in the magnitude of the upper stable equilibrium. A population may be doomed to extinction when extrinsic perturbations, such as habitat loss and fragmentation, reduce the upper equilibrium to levels where environmental or stochastic variation in demographic rates can push the population below its "threshold for establishment."

Discussion

Conservation of primates is occurring at the three different levels of community, population, and individual "genes" (Southwick et al. 1986). Our models may be most directly useful at the single population level. Previous attempts to determine mechanistic causes of local extinction have concentrated upon either demographic stochasticity or inbreeding effects (Ralls & Ballou 1982; Soulé 1987). Our analysis suggests that the relative importance of these factors depends upon social organization. Solitary or monogamous species may have relatively equitable distributions of reproductive success and thus larger effective population sizes than those with less equitable distributions. Nevertheless, these populations will tend to collapse for demographic reasons while at densities that may be higher than those where inbreeding becomes excessively detrimental. In contrast, in gregarious, more promiscuous species, demographic thresholds tend to occur at lower population densities; here, inbreeding may become much more im-

a)
HEALTHY POPULATION

b)
REDUCED ADULT SURVIVAL

c)
STRONG REGULATION b=12

d)
LOSS OF HABITAT
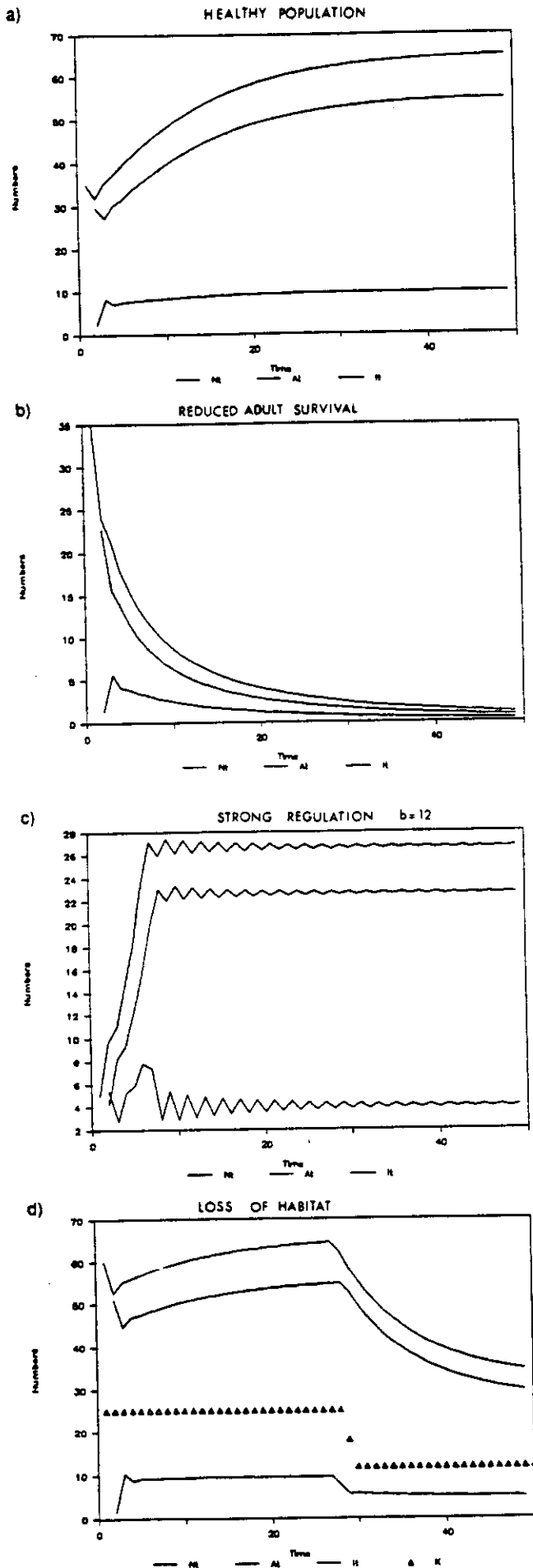
portant, particularly if augmented by inequalities in reproductive success. Exploration of this key point in the demography of endangered primate populations requires both further empirical studies and genetic modeling.

Although the models are analyzed in terms of their properties at equilibrium, we fully appreciate that primate populations are rarely at equilibrium in the wild (Jolly 1985; Richard 1985). The mathematical convenience of undertaking the analysis in this fashion allows us to ascertain properties of the population that apply more generally. Like other age-structured vertebrate populations (Fowler 1981; May 1985), primates are susceptible to both bad years and good years. These produce "gaps" and "pulses" of age cohorts with long-lasting ripples in the population structure. Analyses of these complexities would require considerably larger data sets than are available for most primates. Similarly, we assumed constancy in the inter-birth intervals, while they in fact vary between populations and age at first reproduction may range from two to four inter-birth interval units (Lyles & Dobson 1988). However, the coarse generality (that first reproduction occurs at three inter-birth intervals) presents a useful "rule of thumb" that may be used to determine whether a population is growing or declining after a short period of study.

Determining how an endangered species will respond to perturbation or habitat destruction is an important goal of any conservation study. Table 3 outlines how different types of perturbation affect the model's parameters and how these changes may be used to determine the consequences of similar perturbations to wild primate populations. Above all it is important to realize that small changes in the parameters of the recruitment function may lead to large changes in population density. Thus, the assumption that simple reductions in habitat lead to proportional losses of animals is often naive. For example, if emigration to marginal habitats is an

Figure 11. Four simulations of the models of behavior for different combinations of parameter values; in all cases the upper line is total population, the intermediate line is number of adults, and the lower line is number of infants. (a) Illustrates the case where a population of adults is introduced into an area: s = 0.85, b = 1.0, i = 0.75, and K = 25. (b) Illustrates the effect of reducing adult survival so that λ < 1; s = 0.68, b = 1.0, i = 0.75, K = 25. (c) Illustrates the effect of intense regulation; s = 0.85, b = 12, i = .075, K = 25. (d) Illustrates the effect of a halving of resources on a population close to equilibrium; s = 0.85, b = 1.0, i = 0.75, K = 25 until t = 28, when K drops to 12.

12

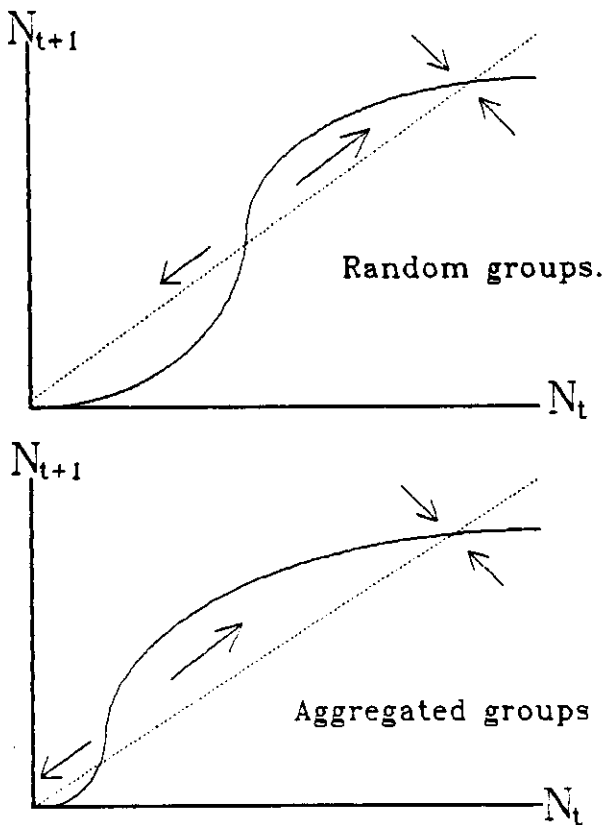*Figure 12. Phase planes of* Nt *against* Nt + 1 *for the model that includes both resource limitation and an Allee effect The upper figure is for a population divided into troops of random size; the lower is for troops that conform to a negative binomial distribution. In both cases the upper right equilibrium is stable, while the lower left equilibrium is unstable. Populations less then this value collapse to extinction.*

important component of population regulation, then loss of these habitats may lead to increased levels of intra-group aggression and changes in the shape of the recruitment function. A potential example of this might be the population of baboons (*Papio cyanocephalus*) in Amboseli National Park, Kenya. Here loss of woodland due to the change in the height of the water table has led to a decrease in suitable habitat and a consequent reduction in population density. However, rates of infant mortality have also increased (Altmann et al. 1985), which may in part reflect changes in the intensity with which the remaining females compete for available resources. Similar effects may be occurring in the primate populations in the fragmented sections of rain forest studied by Lovejoy et al. (1986).

These models may also be adapted to address question of how many individuals may be harvested from a healthy population without serious risk of population

Table 3. The effect of different perturbations on the parameters of the model, the magnitude of the upper equilibrium, N^*, and threshold for establishment, N_T^*.

Perturbation	s	i	F	a	T	δ	k	b	K	N^*	N_T^*
Habitat destruction	?	?	?	?	?	?	?	?	–	– –	??
Habitat fragmentation	?	?	?	?	+	+	?	?	–	– –	+ +
Inclement weather	–	–	–	+	0	+	0	?	?	? ?	+ +
Reduction in food supply	–	–	–	+	?	0	?	+	–	– –	+ +
Increased aggression	–	–	–	+	+	?	+	+	0	– –	+ +
Loss of shelter	–	–	–	+	+	?	+	+	0	– –	+ +
Increase in predators	–	–	–	?	–	?	–	?	?	– ?	– ?
Infectious diseases	–	–	–	?	?	?	+	?	?	– ?	+ ?

This table lists a variety of factors that lead to changes in the basic demographic parameters of primate populations as defined in Table 2. They have been crudely classified into whether they cause increases (+), decreases (−), have no effect (0), or have as yet unknown effects (?) on each of the demographic parameters of the model. Several mechanisms may operate in both ways and some of the factors may act synergistically (e.g., a reduction in the food supply may lead to an increase in aggression). The final two columns give the probable net effect on the magnitudes of the upper stable equilibrium, N^*, and the lower threshold for establishment, N_T^*, illustrated in Figure 12.

collapse. This is a particularly pertinent problem for the biomedical establishment which, in the United States alone, uses more than 50,000 primates in experiments per year (Gay 1986). Roughly half of these are new subjects and about 8,000 primates are born each year in the primate centers (Johnson & Whitehair 1986). The deficit is filled by importing around 17,000 primates annually. The annual imports of long-tailed macaques (*Macaca fascicularis*) to the United States from the Philippines number around 7,000 (Diamond 1985). Unless primate harvests are routinely monitored and regulated, populations are likely to collapse, as has been the case with many fisheries (May 1985). As far as we have been able to establish, no attempts have been made to monitor or manage the wild primate populations exploited by the biomedical profession. Without data on the shape of the recruitment curve (equation 8), it is impossible to determine safe harvest levels. Estimating the magnitude of recruitment function parameters requires long-term sets of population data (at least ten inter-birth intervals). Even when such data is available, the parameters of this function are likely to vary between different habitats, and perhaps also at different times in the same habitat. Similarly, populations with different social structures or different feeding strategies will have different recruitment functions. The prospects

13

for managing even well-studied species are therefore poor.

Conclusions

Identification of the role that demographic forces play in constraining primate social organization remains an important and poorly understood area of primate biology (Altmann & Altmann 1979). Most of the above is a rather straightforward mathematical adumbration of primate population dynamics that has sacrificed considerable detail in an attempt to find a few crude generalities. However, as with a similar attempt to simplify the life histories of marine turtles (Crouse et al. 1987), we feel that the exercise has suggested areas where previously collected data might be reanalyzed, while emphasizing others where different types of data need to be collected. The two most important points to emerge are:

1. Primate populations will tend to collapse when the survival of adult females falls below around 70 percent per inter-birth interval.
2. Species that tend to live in aggregated groups with promiscuous mating will establish and maintain themselves at smaller population densities than species with more solitary and monogamous habits.

Even these conclusions err on the side of cautious optimism. In a real stochastic world, pessimism may be the better strategy. Any attempts to manage endangered populations using the preceding mathematical models should allow a healthy margin of safety. This might most readily be achieved by hybridizing the models with the stochastic BIDE (birth/immigration/death/emigration) models developed by Cohen (1969, 1971, 1972).

Future collections of long-term data for most primate species are threatened by habitat destruction. These data are needed to estimate basic demographic rates and shapes of recruitment functions. In the absence of data for a species, it will be necessary to extrapolate the critical data from populations for which long-term records are available. Comparative data from many species may then be used to assess the relative importance of different behavioral mechanisms in determining the shape of these demographic functions. Understanding how behavioral mechanisms affect population dynamic processes remains a formidable challenge to behavioral ecologists (Hassell & May 1985). More studies should address the problems of how the available data on food and habitat choice convert into functions that determine recruitment. At a time when 58 percent of the world's primate species are listed as endangered (1988 IUCN Red List of Threatened Species), it remains of paramount importance that conservation strategies for primates merge the enormous field knowledge of the primatologist with the generalized simplifications of the population biologist.

Literature Cited

Allee, W. C. 1931. Animal aggregations. A study in general sociology. University of Chicago Press, Chicago, Illinois.

Altmann, S. A., and J. Altmann. 1979. Demographic constraints on behavior and social organization. Pages 47–64 in I. S. Bernstein and E. O. Smith, editors. Primate ecology and human origins: ecological influences on social organization. Garland STPM Press, New York.

Altmann, J., S. A. Altmann, and G. Hausfater. 1981. Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. American Journal of Primatology 1:389–399.

Altmann, J., S. A. Altmann, G. Hausfater, and S. A. McCusky. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. Primates 18:315–330.

Altmann, J., G. Hausfater, and S. A. Altmann. 1985. Demography of Amboseli baboons. American Journal of Primatology 8:113–125.

Beddington, J. R. 1974. Age distribution and the stability of simple discrete time population models. Journal of Theoretical Biology 47:65–74.

Benirschke, K., editor. 1986. Primates: The Road to Self-Sustaining Populations. Springer-Verlag, New York.

Bourliere, F. 1985. Primate communities: their structure and role in tropical ecosystems. International Journal of Primatology 6:1–26.

Butynski, T. M. 1982. Harem-male replacement and infanticide in the blue monkey (*Cercopithecus mitus stuhlmanni*) in the Kibale Forest, Uganda. American Journal of Primatology 3:1–22.

Carpenter, C. R. 1962. Field studies of a primate population. Pages 286–294 in E. L. Bliss, editor. Roots of behaviour. Harper, New York.

Cheney, D. L. 1987. Interactions and relationships between groups. Pages 267–281 in B. B. Smuts, D. L. Cheney, R. M. Sey-

14

farth, R. W. Wrangham, and T. T. Struhsaker, editors. Primate societies. Universities of Chicago Press, Chicago, Illinois.

Cheney, D. L., P. C. Lee, and R. M. Seyfarth. 1981. Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. Behavioral Ecology and Sociobiology 9:153–161.

Cohen, J. E. 1969. Natural primate troops and a stochastic population model. American Naturalist 103:455–478.

Cohen, J. E. 1971. Casual groups of monkeys and men: stochastic models of elemental social systems. Harvard University Press, Cambridge, Massachusetts. 175 pp.

Cohen, J. E. 1972. Markov population processes as models of primate social and population dynamics. Theoretical Population Biology 3:119–134.

Cohen, J. E. 1975. The size and composition of social groups of wild orang-utans. Animal Behaviour 23:543–550.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

Deag, J. M. 1984. Demography of the Barbary macaque at Ain Kahla in the Moroccan Moyen Atlas. Pages 113–133 in J. E. Fa, editor. The Barbary macaque. Plenum Press, New York.

Diamond, J. M. 1985. Future of the world's primates. Nature 317:577–578.

Dittus, W. P. J. 1975. Population dynamics of the Toque monkey, *Macaca sinica*. Pages 125–152 in R. H. Tuttle, editor. Sociology and psychology of primates. Mouton Publishers, The Hague, Netherlands.

Dittus, W. P. J. 1977. The social regulation of population density and age-sex distribution in the Toque monkey. Behaviour 63:281–322.

Dittus, W. P. J. 1979. The evolution of behaviours regulating density and age-specific sex ratios in a primate population. Behaviour 69:265–301.

Dittus, W. P. J. 1980. The social regulation of primate populations. Pages 263–268 in D. Lindberg, editor. The macaques: studies in ecology, behaviour and evolution. Van Nostrand Reinhold, New York.

Drickamer, L. C. 1974. A ten year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatologia 21:61–80.

Dukelow, W. R. 1983. Membership analysis of the first six years of the American Society of Primatologists. American Journal of Primatology 4:319–322.

Dunbar, R. I. M. 1980. Demographic and life history variables of a population of gelada baboons (*Theropithecus gelada*). Journal of Animal Ecology 49:485–506.

Dunbar, R. I. M. 1987. Demography and reproduction. Pages 240–249 in B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, editors. Primate societies. University of Chicago Press, Chicago, Illinois.

Fa, J. E. 1984. Structure and dynamics of the Barbary macaque population in Gibraltar. Pages 263–306 in J. E. Fa, editor. The Barbary macaque. Plenum Press, New York.

Fairbanks, L. A., and M. T. McGuire. 1984. Determinants of fecundity and reproductive success in captive vervet monkeys. American Journal of Primatology 7:27–38.

Fedigan, L. M. 1983. Dominance and reproductive success in primates. Yearbook of physical anthropology 26:91–130.

Fedigan, L. M., H. Gouzoules, and S. Gouzoules. 1983. Population dynamics of Arashiyama West Japanese macaques. International Journal of Primatology 4:307–321.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

Froehlich, J. W., R. W. Thorington, Jr., and J. S. Otis. 1981. The demography of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. International Journal of Primatology 2:207–236.

Galat, G., and A. G. Galat-Luong. 1977. Demographie et regime alimentaire d'une troupe de *Cecopithecus aethiops sabaeus*. La terre et la vie 31:557–577.

Galdikas, B. M. F. 1981. Orangutan reproduction in the wild. Pages 281–300 in C. E. Graham, editor. Reproductive biology of the great apes. Academic Press, New York.

Gartlan, J. S. 1969. Sexual and maternal behaviour of the vervet monkey, *Cercopithecus aethiops*. Journal of Reproduction and Fertility Supplement 6:137–150.

Gay, W. I. 1986. Research uses and projections of nonhuman primates as research subjects. Pages 513–520 in K. Benirschke, editor. Primates. The road to self-sustaining populations. Springer-Verlag, New York.

Glander, D. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. American Journal of Physical Anthropology 53:25–36.

Goodall, J. 1983. Population dynamics during a 15-year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. Zeitschrift Für Tierpsychologie 61:1–60.

Gouzoules, H., S. Gouzoules, and L. Fedigan. 1982. Behavioural dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). Animal Behaviour 30:1138–1150.

Harcourt, A. H., D. Fossey, and J. Sabater-Pi. 1981. Demography of *Gorilla gorilla*. Journal of Zoology, London. 195:215–233.

Harvey, P. H., and T. H. Clutton-Brock. 1985. Life history variation in primates. Evolution 39:559–581.

Hassell, M. P., and R. M. May. 1985. From individual behaviour to population dynamics. Pages 3–32 in R. M. Sibly and R. H. Smith, editors. Behavioral ecology: ecological consequences of adaptive behaviour. Blackwell Scientific, Oxford, England.

Hiraiwa-Hasegawa, M., T. Hasegawa, and T. Nishida. 1984. Demographic study of a large-sized unit-group of chimpanzees in

15

the Mahale Mountains, Tanzania: a preliminary report. Primates 25:401–413.

Horrocks, J. A. 1986. Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaeus*) in Barbados, West Indies. International Journal of Primatology 7:31–47.

Hrdy, S. B. 1977. The Langurs of Abu. Harvard University Press, Cambridge, Massachusetts.

Ikeda, H. 1982. Population changes and ranging behaviour of wild Japanese monkeys at Mt. Kawaradake in Kyushu, Japan. Primates 23:338–347.

Itani, J. 1975. Twenty years with Mount Takasaki monkeys. Pages 101–125 in G. Bermant and D. G. Lindburg, editors. Primate utilization and conservation. John Wiley & Sons, New York.

Janson, C. H., and C. P. van Schaik. 1988. Recognizing the many faces of primate food competition: methods. Behaviour 105:165–186.

Johnsen, D. O., and L. A. Whitehair. 1986. Research facility breeding. Pages 499–511 in K. Benirschke, editor. Primates: the road to self-sustaining populations. Springer-Verlag, New York.

Jolly, A. 1985. The evolution of primate behavior. 2nd ed. Macmillan, New York.

Jones, M. L. 1986. Successes and failures of captive breeding. Pages 251–260 in K. Benirschke, editor. Primates: the road to self-sustaining populations. Springer-Verlag, New York.

Keiding, N. 1977. Statistical comments on Cohen's application of a simple stochastic population model to natural primate troops. American Naturalist 111:1211–1219.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. Bioscience 39:152–161.

Koford, C. B. 1965. Population dynamics of rhesus monkeys on Cayo Santiago. Pages 160–174 in I. DeVore, editor. Primate behavior. Holt, Rinehart and Winston, New York.

Koyama, N. 1980. Demography of Japanese monkeys. Pages 9–34 in L Asahi, editor. Seeking the Japanese wild animals. Tokai University Press, Tokyo, Japan.

Koyama, N., K. Norikoshi, and T. Mano. 1975. Population dynamics of Japan monkeys at Arashiyama. Pages 411–417 in Contemporary Primatology. 57th International Congress of Primatology. Karger, Basel, Switzerland.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1–18.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245.

Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soulé, editor. Conservation biology. The science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Lyles, A. M., and A. P. Dobson, 1988. The population biology of provisioned and un-provisioned primate populations. Pages 167–198 in J. E. Fa and C. H. Southwick, editors. Ecology and behavior of food-enhanced primate groups. Alan R. Liss, New York.

Lyles, A. M., and R. M. May. 1987. Problems in leaving the ark. Nature 326:245–246.

Mackinnon, J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). Animal Behavior 22:3–74.

Malik, I., P. K. Seth, and C. H. Southwick. 1984. Population growth of free-ranging rhesus monkeys at Tuglaqabad. American Journal of Primatology 7:311–321.

Maruhasi, T. 1982. An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 23:317–337.

May, R. M. 1977. Togetherness amongst schistosomes: its effects on the dynamics of the infection. Mathematical Biosciences 35:301–343.

May, R. M., editor. 1985. Exploitation of marine communities. Springer-Verlag, Berlin, East Germany.

May, R. M., and A. M. Lyles. 1987. Living Latin binomials. Nature 326:642–643.

McGuire, M. T. 1974. The St. Kitts vervet. Contributions to Primatology, vol. 1. Karger, New York.

Melnick, D. 1981. Microevolution in a population of Himalayan rhesus monkeys (*Macaca mulatta*). Ph.D. diss., Yale University.

Menard, N., D. Vallet, and A. Gautier-Hion. 1985. Demographie et reproduction de Macaca sylvanus dans differents habitats en Algerie. *Folia Primatologia* 44:65–81.

Milton, K. 1981. Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*. Primates 22:574–579.

Mittermeier, R. A. 1986. Strategies for the conservation of highly endangered primates. Pages 1013–1022 in K. Benirschke, editor. Primates: the road to self-sustaining populations. Springer-Verlag, New York.

Mittermeier, R. A., J. F. Oates, A. E. Eudey, and J. Thornback. 1986. Primate conservation. Pages 3–72 in G. Mitchell, and J. Erwin, editors. Comparative primate biology, vol. 2, Part A. Alan R. Liss, New York.

Mori, A. 1979. Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. Primates 20:371–397.

/ 6

National Research Council (USA) Committee on Non-Human Primates. 1981. Techniques for the study of primate population ecology. National Academy Press, Washington, D.C.

Newton, P. N. 1986. Infanticide in an undisturbed forest population of hanuman langurs, *Presbytis entellus*. Animal Behaviour 34:785–789.

Ohsawa, H. 1979. Herd dynamics. Pages 47–80 in M. Kawai, editor. Ecological and sociological studies of gelada baboons. Contributions to primatology, vol. 16. Karger, Basel, Switzerland.

Ohsawa, H., Y. Sugiyama, and A. Nishimura. 1977. Population dynamics of Japanese monkeys at Takasakiyama by the marking trace. (In Japanese.) Pages 19–36 in Y. Sugiyama, editor. Population dynamics of Japanese monkeys at Takasakiyama. Oita, Oita City, Japan.

Paul, A., and D. Thommen. 1984. Timing of birth, female reproductive success and infant sex ratio in semifree-ranging Barbary macaques (*Macaca sylvanus*). Folia Primatologia 42:2–16.

Ralls, K., and J. Ballou. 1982. Effects of inbreeding on infant mortality in captive primates. International Journal of Primatology 3:491–505.

Rawlins, R. G., M. J. Kessler, and J. E. Turnquist. 1984. Reproductive performance, population dynamics and anthropometrics of the free-ranging Cayo Santiago rhesus macaques. Journal of Medical Primatology 13:247–259.

Rawlins, R. G., and M. J. Kessler. 1986. Demography of the free-ranging Cayo Santiago macaques. 1976–1983. Pages 47–72 in R. G. Rawlings and M. J. Kessler, editors. The Cayo Santiago macaques. History, behavior & biology. State University of New York, Albany, New York.

Richard, A. F. 1985. Primates in nature. W. H. Freeman and Company, New York.

Scucchi, S. 1984. Interbirth intervals in a captive group of Japanese macaques. Folia Primatologia 42:203–208.

Sheperd, J. G. 1982. A family of general production curves for exploited populations. Mathematical Biosciences 59:77–93.

Sigg, H., A. Stolba, J.-J. Abegglen, and V. Dasser. 1982. Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. Primates 23:473–487.

Silk, J. B. 1987. Social behavior in evolutionary perspective. Pages 318–329 in B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, editors. Primate societies. University of Chicago Press, Chicago, Illinois.

Smith, D. G. 1982. A comparison of the demographic structure and growth of free-ranging and captive groups of rhesus monkeys (*Macaca mulatta*). Primates 23:24–30.

Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker. 1987. The order primates: species names and a guide to social organization. Pages 499–505 in B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struh-

saker, editors. Primate societies. University of Chicago Press, Chicago, Illinois.

Soini, P. 1982. Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. Folia Primatologia 39:1–21.

Soulé, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, New York. 189 pp.

Southwick, C. H., R. A., Mittermeier, J. G. Robinson, and R. A. Tenaza. 1986. Report of the American Society of Primatologists subcommittee on the status of primates in the wild. American Journal of Primatology 10:371–378.

Southwick, C. H., T. Richie, H. Taylor, H. J. Teas, and M. F. Siddiqi. 1980. Rhesus monkey populations in India and Nepal: patterns of growth, decline, and natural regulation. Pages 151–170 in M. N. Cohen, R. S. Malpass, and H. G. Klein, editors. Biosocial mechanisms of population regulation. Yale University Press, New Haven, Connecticut.

Southwick, C. H., and R. B. Smith. 1986. The growth of primate field studies. Pages 73–91 in G. Mitchell and J. Erwin, editors. Comparative primate biology, vol. 2, part A. Alan R. Liss, New York.

Strum, S. C., and J. D. Western. 1982. Variations in fecundity with age and environment in olive baboons (*Papio anubis*). American Journal of Primatology 3:61–76.

Sugiyama, Y. 1965. Behavioral development and social structure in two troops of hanuman langurs (*Presbytis entellus*). Primates 6:213–247.

Sugiyama, Y. 1984. Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976 and 1983. Primates 25:391–400.

Sugiyama, Y., and H. Ohsawa, 1982. Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. Folia Primatologia 39:238–263.

Suzuki, A., K. Wada, S. Yoshiro, E. Tokita, S. Hara, and Y. Aburada. 1975. Population dynamics and group movement of Japanese monkeys in Yokoyugawa valley, Shiga Heights. (In Japanese.) Physiological Ecology 16:15–23.

Takahata, Y. 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. Primates 21:303–329.

Tanaka, T., K. Tokuda, and S. Kotera. 1970. Effects of infant loss on the interbirth interval of Japanese monkeys. Primates 11:113–117.

Teas, J., T. L. Richie, H. G. Taylor, M. F. Siddiqi, and C. H. Southwick. 1981. Natural regulation of rhesus monkey populations in Kathmandu, Nepal. Folia Primatologia 35:117–123.

Terborgh, J. 1983. Five New World primates. Princeton University Press, Princeton, New Jersey.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 in M. E. Soulé, editor. Conservation biology. The science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

17