

NATURAL PRIMATE TROOPS AND A STOCHASTIC
POPULATION MODEL

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INTRODUCTION

The purpose of this paper is to show that existing data on the sizes of free-ranging troops of nonhuman primates are orderly in a way not previously recognized, and that stochastic models of theoretical populations can account for much of the order.

Stochastic models can describe the fluctuations in size of theoretical populations whose individuals are born, immigrate, and die or emigrate. As such models have been developed, primarily during the last thirty years, field biologists have been independently studying the behavior, composition, and size of natural primate troops.

This paper will summarize the assumptions and predictions of the simplest birth-immigration-death-emigration (BIDE) model and compare them with available information on free-ranging apes (gibbons, *Hylobates*), Old World monkeys (black and white colobus, *Colobus guereza*; hanuman langurs, *Presbytis entellus*; and baboons, *Papio*), and New World monkeys (howlers, *Alouatta palliata*).

The success of the equilibrium state of the BIDE model in describing the distribution of size of troops of these species will suggest that the model is one approximation to the natural dynamics of primate troops. The only available data on the actual gains and losses of individuals in one particular baboon troop will suggest that further theoretical development is needed to describe in detail the dynamics of troop size or that more data are needed, or both.

The statistical tool used to assess the variability of the few available vital statistics on baboons is the "jackknife," a technique of enormous versatility and power which seems to be new to biology. An appendix to this paper describes the technique (though not its rationale) and its application.

THE STOCHASTIC MODEL

The following review of the assumptions of the BIDE model and its predictions uses the notation of Bailey (1964, pp. 91–101), who proves the assertions made. Several other expositions are available (Kendall 1949; Bartlett 1955, 1960; Parzen 1962).

Suppose a theoretical population contains $X(t)$ individuals at time $t \geq 0$, where $X(t)$ is some nonnegative integer and t is continuous. Suppose that the chance of any individual in the population giving birth to a single other individual in time Δt is $\lambda \Delta t$ and that all births are mutually independent. Then the probability of a single birth from any of the $X(t)$ individuals in the population is $\lambda X(t) \Delta t$. Suppose in addition that there is a random stream of immigrants at a mean rate v which is independent of the current size of the population. Thus the chance that the population size increases by one in the interval Δt is the sum of the chances of increase due to birth and immigration, namely, $\lambda X(t) \Delta t + v \Delta t + o(\Delta t)$. Here $o(\cdot)$ is any function such that $o(\Delta t)/(\Delta t)$ approaches zero as Δt approaches zero; $o(\cdot)$ may represent a different function each time it appears.

In addition, suppose that the chance for any individual of dying in the interval Δt is $\mu_1 \Delta t$, and that any individual's chance of emigrating from the population in Δt is $\mu_2 \Delta t$. Then, again under the assumption of mutual independence, the probability that the population will decrease by one in time Δt is proportional to the total size of the population $X(t)$. If the death and emigration rates are combined into a single loss rate $\mu = \mu_1 + \mu_2$, the chance of one loss due to death or emigration in Δt is $\mu X(t) \Delta t + o(\Delta t)$. From the assumption that the chance of more than one birth, immigration, or death or emigration in a short time interval Δt is $o(\Delta t)$, it follows that the chance of no change in the population size in Δt is equal to $1 - (\lambda + \mu) X(t) \Delta t - v \Delta t + o(\Delta t)$.

We suppose that a theoretical population is initially of size zero and is started off by an immigrant. It may be shown that the average or expected population size will grow infinitely in time unless the birth rate λ is less than the loss rate μ (Bailey 1964, p. 99). Since the collections of primate troops I will review have presumably existed for a long time, yet are assumed to have a distribution which is stable in time (barring catastrophic influences) or which is approaching stability, we make the assumption that $\lambda < \mu$.

Then if birth, death or emigration, and immigration are all proceeding at strictly positive rates, it may be shown that the probability $p_{NB}(k)$ that the theoretical population contains exactly k individuals after a long time t is independent of time and the initial population size and is given by the negative binomial distribution:

$$p_{NB}(k) = \binom{r+k-1}{k} p^r q^k, \quad k = 0, 1, 2, \dots, \quad (1)$$

where the parameters r , p , and $q = 1 - p$ are related to the parameters of the BIDE model by

$$r = v/\lambda, \quad q = 1 - p = \lambda/\mu. \quad (2)$$

If the birth rate λ is reduced to zero, so that the population is maintained by a balance of immigration and death or emigration, then it may be shown that the probability $p_P(k)$ that the population contains exactly k individuals

after a long time t is again independent of time and is given by the Poisson distribution:

$$p_P(k) = e^{-m} m^k/k!, \quad k = 0, 1, 2, \dots, \quad (3)$$

where the parameter m is related to the parameters of the BIDE model by

$$m = v/\mu. \quad (4)$$

Another interpretation of this situation, where $\lambda = 0$, is that birth is occurring at a rate which is independent of the total size of the population (aside from whatever immigration may or may not be occurring). Thus if there were a fixed number of mothers in a theoretical population, regardless of the number of males or children, then one would require $\lambda = 0$ and v positive.

APPLYING THE MODEL

In the following applications, the theoretical population of the BIDE model will be identified with a troop of primates. Two terminological snares should be avoided.

First, the theoretical population in the BIDE model is called a "population" because of the traditional statistical terminology for such models. I am not identifying this theoretical population with what an ecologist or population geneticist would call a (genetic or local) population, namely "the community of potentially interbreeding individuals at a given locality" (Mayr 1963, p. 136). The genetic population of howler monkeys on Barro Colorado Island, for example, is a collection of troops, each of which will be viewed as an independent replicate of a single theoretical population described by the BIDE model. Under this interpretation, "immigration" in the BIDE model means only that an animal entered a troop. The entrant may have shifted from another troop in the same genetic population, in which case no immigration in the genetic sense has occurred, or may have entered the troop and the genetic population from outside—immigration in both senses. The distribution of sizes of troops, not of genetic populations, will be compared with the predicted distributions of the BIDE model.

Second, some authors call troops "social groups." But these are different from the social (sub)groups, sleeping (sub)groups, or coalitions within a troop described by Struhsaker (1967), among others. Just as troops make up a genetic population, social (sub)groups make up a troop, and individuals make up a social (sub)group. Alleged troops such as those of colobus and gibbon may have smaller average size than, say, vervet sleeping (sub)groups; but stochastic models for the size of social (sub)groups (Cohen 1969) should not be confused with models for troop size.

The BIDE model assumes that the rates λ , μ , and v are constant in time. This assumption may be acceptable when size distributions are available at only one time (as is the case for the gibbons, colobus, langurs, and baboons). When observations repeated over a long period of time are available (as

for the howlers), identifiable external influences (such as an epidemic) will make it necessary to abandon the assumption.

This simple model also assumes that all of the parameters apply equally and independently to all of the individuals in the theoretical population. In a real troop not all individuals are equally likely to give birth or die, to immigrate or emigrate; the rates of these processes are age- and sex-dependent. However, if, for example, half of the individuals in the troop have a true rate $\lambda' = 2\lambda$ of giving birth to another individual, while the remaining half of the population has a zero birth rate, then the birth rate of the whole troop may be taken as the average $(2\lambda + 0)/2 = \lambda$. This averaging is permissible as long as the birth process does not interact with the other death and migration processes, that is, as long as, for example, neonates die and migrate at the same average rate as individuals of any age. The simplifying assumption that on the average the constant parameters apply equally and independently to all individuals of the troops will suffice until the data do not confirm the consequences of this assumption.

ESTIMATION AND GOODNESS OF FIT

In order to compare observed distributions of troop sizes with those predicted by the BIDE model, it is necessary to estimate the parameters of the theoretical distributions.

For the Poisson distribution, m was set equal to the observed mean \bar{x} ; this is the ordinary maximum-likelihood estimate of m ("ordinary" in the sense of Kendall and Stuart 1961, chap. 30). For the Poisson distribution in which the zero value was unobservable (called the 0-truncated Poisson), the ordinary maximum-likelihood estimate \hat{m}_0 of m was obtained from the observed mean \bar{x} by using the tables of Cohen (1960). For the Poisson distribution in which both $X(t) = 0$ and $X(t) = 1$ were unobservable (the 0,1-truncated Poisson), the estimator \hat{m}_1 of m devised by Subrahmaniam (1965) was used:

$$\hat{m}_1 = \bar{x} - 2f(2)/N, \quad (5)$$

where $f(k)$ is the observed frequency of k counts (here $f[0] = f[1] = 0$) and N is the total number of observations. Subrahmaniam showed equation (5) to be asymptotically nearly completely efficient for a wide range of values of m . This unbiased estimator resulted in better fits to the data than did the estimator proposed by Rider (1953), which I also tried.

For the negative binomial distribution in which zero values were unobservable (referred to here as the truncated negative binomial distribution), the parameters were estimated by the method of Brass (1958):

$$\hat{p} = \bar{x}(1 - f(1)/N)/s^2, \quad \hat{r} = (\hat{p}\bar{x} - f(1)/N)/(1 - \hat{p}), \quad (6)$$

where s^2 is the sample variance.

To decide how well the fitted distributions using these estimators describe the observed distributions, it is necessary to attach probability values to the usual X^2 statistic for goodness for fit,

$$X^2 = \sum_{i=1}^K (O(i) - E(i))^2/E(i),$$

where the observations have been lumped into K classes, i runs over these classes, and $O(i)$ and $E(i)$ are the observed and expected frequencies in each class, respectively. The use of expected class frequencies as small as 1 in the tails of Poisson and negative binomial distributions is justified by Cochran (1954).

When ordinary maximum-likelihood estimators are used, as for the Poisson and 0-truncated Poisson, the distribution of X^2 in equation (7) is bounded between a χ_{k-1}^2 and a χ_{k-2}^2 variable, where the subscript shows the number of degrees of freedom. As K becomes large, the difference between the two can be ignored (Kendall and Stuart 1961, p. 430). In these cases, if a fit is not rejected assuming $K - 2$ degrees of freedom, it will certainly not be rejected using $K - 1$ degrees of freedom; so it is only in cases of marginal fits that the distribution of χ_{k-1}^2 needs to be considered.

When estimators other than maximum likelihood or minimum χ^2 are used, as for the 0,1-truncated Poisson and truncated negative binomial distributions, it can only be said that X^2 has a distribution with "more" degrees of freedom than $K - \Theta - 1$, where Θ is the number of parameters estimated. Hence if a fit is accepted using the distribution of $\chi_{K-\Theta-1}^2$ it would also be accepted using the correct distribution. Cases only marginally rejected (say, at the .05-.01 level) using $K - \Theta - 1$ degrees of freedom remain doubtful.

When the number of observations in a frequency distribution is small, a way of testing for deviations from the Poisson distribution which is more powerful than fitting a theoretical distribution to the observed is to compare the observed dispersion with the expected. According to the Poisson variance test devised by Fisher (see Cochran 1954), for large samples

$$X^2 = \frac{(N - 1) s^2}{\bar{x}} \tag{8}$$

should asymptotically have the distribution of χ_{N-1}^2 if the distribution from which the independent observations came is Poisson. Similarly (Rao and Chakravarti 1956), if \hat{m}_0 is the maximum-likelihood estimate of the parameter of the 0-truncated Poisson distribution, then for large samples

$$X^2 = \frac{(N - 1) s^2}{(1 - p_1) \bar{x}}, \quad \text{where } p_1 = \frac{\hat{m}_0}{(e^{\hat{m}_0} - 1)}, \tag{9}$$

should also asymptotically have the distribution of χ_{N-1}^2 .

HOWLER MONKEYS

For the collection of howler monkey troops (*Alouatta palliata*) living on Barro Colorado Island in the middle of the Panama Canal, extensive data based on his own and others' observations have been collected by Carpenter (1962).

In 1932 and 1933 Carpenter attempted to census the size and composition by sex and maturity of all troops on the island (in primate studies "maturity" usually means size and sexual development and may differ from chronological age). In 1935 Carpenter censused a sample of 15 troops. In 1951, a few years after an epidemic (possibly yellow fever) had killed a substantial part of the howler population, N. Collias and C. Southwick attempted a complete census of the monkeys. Finally, in 1959, Carpenter, Mason, and Southwick censused the entire island. The five size distributions resulting from these counts, numbered in chronological order, are presented in table 1.

Three fitted distributions are presented in table 2. The first shows that the sum of all the observed distributions may be described by the truncated negative binomial distribution. But examination of the means and variances of the five observed distributions (bottom of table 1) shows that the 1951 census, after the epidemic, differs grossly from the other four counts, which are quite similar. Hence table 2 also presents a fit of the truncated negative binomial distribution to the sum of the first, second, third, and fifth observed counts and a separate fit of the truncated Poisson distribution to the fourth (postepidemic) census. While the one-parameter truncated Poisson distribution is sufficient to describe the postepidemic observations, it is not sufficient for any of the other distributions. Except for the postepidemic census of 1951, the variance of troop size was too large compared to the mean troop size for the observations in each census separately to have come from a truncated Poisson distribution, according to a one-tailed application of the truncated Poisson variance test (equation [9]) at the .01 level.

The probability level attached to X^2 for the pooled distributions in table 2 should be taken as a lower bound on the probability that a worse fit to the predicted distribution would have occurred by chance, rather than as an exact value. The probability value overstates the significance of any discrepancy between observed and predicted distributions because the observations that go into the two pooled distributions I and II in table 2 are not independent. The three counts made by Carpenter within three years are especially nonindependent. The finding that the observed distributions can be described by the theoretical in spite of this lack of independence means that greater confidence can be attached to the agreement than the probability levels would suggest.

If the four nonepidemic counts are typical of the steady-state size distribution of howler troops, and if the BIDE model is valid, then the estimated parameters show that the ratio of the mean rate of immigration to the mean birth rate per individual is approximately 7.05. Similarly, the ratio of the

TABLE 1
FREQUENCY DISTRIBUTIONS OF SIZE OF HOWLER TROOPS*

| Size | 1932 (1) | 1933 (2) | 1935 (3) | 1951 (4) | 1959 (5) |
|-----------|-------------|-------------|-------------|-------------|-------------|
| 1..... | ... | ... | ... | ... | ... |
| 2..... | ... | ... | ... | 1 | ... |
| 3..... | ... | ... | ... | 1 | 1 |
| 4..... | 1 | 1 | ... | 3 | 3 |
| 5..... | 1 | 1 | ... | 4 | ... |
| 6..... | ... | 1 | 1 | 1 | 1 |
| 7..... | ... | ... | 1 | 6 | ... |
| 8..... | ... | 1 | ... | 1 | ... |
| 9..... | ... | ... | 1 | 3 | 1 |
| 10..... | 1 | 1 | ... | 4 | 1 |
| 11..... | 1 | 1 | ... | 2 | 2 |
| 12..... | ... | 1 | ... | 2 | 3 |
| 13..... | 1 | 1 | ... | ... | 2 |
| 14..... | 3 | 1 | ... | ... | 4 |
| 15..... | 3 | 2 | ... | ... | 1 |
| 16..... | ... | ... | 2 | 1 | 1 |
| 17..... | ... | 1 | ... | 1 | 1 |
| 18..... | 3 | 2 | 2 | ... | 4 |
| 19..... | 2 | 2 | 2 | ... | 2 |
| 20..... | 2 | 2 | 1 | ... | ... |
| 21..... | ... | 2 | 1 | ... | 1 |
| 22..... | 1 | ... | 1 | ... | 2 |
| 23..... | ... | 2 | 1 | ... | 2 |
| 24..... | 1 | 1 | ... | ... | 2 |
| 25..... | ... | 2 | 1 | ... | 1 |
| 26..... | ... | ... | ... | ... | ... |
| 27..... | 1 | 2 | ... | ... | 1 |
| 28..... | 1 | ... | ... | ... | 3 |
| 29..... | ... | 1 | ... | ... | ... |
| 30..... | ... | ... | ... | ... | ... |
| 31..... | ... | ... | ... | ... | ... |
| 32..... | ... | ... | ... | ... | 1 |
| 33..... | ... | ... | ... | ... | 1 |
| 34..... | ... | ... | 1 | ... | 1 |
| 35..... | 1 | ... | ... | ... | ... |
| 36..... | ... | ... | ... | ... | ... |
| 37..... | ... | ... | ... | ... | 1 |
| 45..... | ... | ... | ... | ... | 1 |
| \bar{x} | 17.304 | 17.464 | 18.200 | 7.967 | 18.500 |
| s^2 | 49.949 | 48.332 | 51.029 | 12.723 | 88.070 |

* Data are from Carpenter (1962).

mean birth rate to the mean loss (death plus emigration) rate is estimated at 0.72.

An estimate of the mean birth rate per individual per year (which will be lower than the mean birth rate per adult female) may be obtained by finding the ratio (number of individuals in category "infant 1")/(total number of other individuals in the troop) for each troop, as listed in Carpenter (1962), and then averaging over all troops. I assume that "infant 1" means an infant born in the last year. This calculation yields the estimates $\lambda_{1932} = 0.0440$, $\lambda_{1933} = 0.0428$, $\lambda_{1959} = 0.0475$, and an average weighted by the number of groups in each census, $\lambda = 0.0453$ per individual per year. But there is no obvious way to get independent estimates of the

TABLE 2
SUMMED FREQUENCY DISTRIBUTIONS OF SIZE OF HOWLER TROOPS*

| I† (ALL 5 YEARS) | | | II (ALL BUT 1951) | | | III (1951) | | |
|---------------------|-----------------------|-------|----------------------|--------------------|-------|---------------|----------------------|-------|
| Size | Obs. | Pred. | Size | Obs. | Pred. | Size | Obs. | Pred. |
| 1-5 | 17 | 10.2 | 1-5 | 8 | 2.9 | 1-3 | 2 | 1.3 |
| 6-10 | 25 | 30.4 | 6-10 | 10 | 16.1 | 4 | 3 | 1.8 |
| 11-15 | 30 | 36.1 | 11-15 | 26 | 27.7 | 5 | 4 | 2.8 |
| 16-20 | 31 | 28.3 | 16-20 | 29 | 26.8 | 6 | 1 | 3.7 |
| 21-25 | 21 | 17.6 | 21-25 | 21 | 18.4 | 7 | 6 | 4.2 |
| 26-30 | 9 | 9.4 | 26-30 | 9 | 10.1 | 8 | 1 | 4.2 |
| 31-35 | 5 | 4.6 | 31-35 | 5 | 4.8 | 9 | 3 | 3.7 |
| 36-40 | 1 | 2.0 | 36-40 | 1 | 2.0 | 10 | 4 | 2.9 |
| 41- | 1 | 1.4 | 41- | 1 | 1.2 | 11 | 2 | 2.1 |
| ... | ... | ... | ... | ... | ... | 12 | 2 | 1.4 |
| ... | ... | ... | ... | ... | ... | ≥ 13 | 2 | 1.9 |
| | $\bar{x} = 15.807$ | | | $\bar{x} = 17.945$ | | | $\bar{x} = 7.967$ | |
| | $s^2 = 69.437$ | | | $s^2 = 63.630$ | | | $s^2 = 12.723$ | |
| | $\hat{p} = 0.2276$ | | | $\hat{p} = 0.2820$ | | | $\hat{m}_0 = 7.9572$ | |
| | $\hat{r} = 4.6590$ | | | $\hat{r} = 7.0492$ | | | | |
| | $X^2 = 8.233$ | | | $X^2 = 12.437$ | | | $X^2 = 7.339$ | |
| | df = 6 | | | df = 6 | | | df = 9 | |
| | $P\dagger = (.2, .3)$ | | | $P = (.05, .1)$ | | | $P = (.5, .7)$ | |

* Data are from table 1.

† Obs. = observed; Pred. = predicted.

‡ In this and all subsequent tables P = the probability of a worse fit to the *theoretical* distribution by chance alone.

immigration and loss rates in order to check the parameters of the fitted distribution.

It is reassuring to find that if the counted 1932 population of 398 monkeys grew at the estimated $\lambda \sim 4.5$ percent for 27 years, it would number approximately 1,310 monkeys, well beyond the total of 814 monkeys observed in 1959. What is difficult to account for is the 23 percent increase in population Carpenter reported between 1932 and 1933. It seems likely to me that part of this increase should be attributed to censusing error. Carpenter's guesses that his 1932 total population estimate of 398 had a sampling error of ± 50 and that his 1933 estimate of 489 had a sampling error of ± 25 take account of this possibility. (I thank Stuart Altmann for pointing this out.)

The epidemic before 1951 struck most heavily among the nonreproductive infants and juveniles, according to the counts of Collias and Southwick. Hence it is not surprising that shortly after the epidemic the size distribution appeared as if no births had taken place, only immigration to particular troops (not to the island) contributing to increased size. From the observation that even the smallest troops had at least one adult male after the epidemic, Carpenter (1962) infers that there must have been substantial migration among troops after the epidemic. Since the epidemic left alive relatively more reproductive females, it is perhaps also reasonable that the average net rate of reported growth sustained by the population between 1951 and 1959 was 16 percent per year.

The observers of the howlers recorded (or estimated) the numbers of animals in each troop in each of nine classes: males (adult), females (adult)

without young, females with young, infants in three maturity classes, and juveniles in three maturity classes (with no sex differentiation among infants and juveniles). Each year the number of individuals in one of these classes, such as "infant 1," increases at a rate which does not depend on

TABLE 3
MEANS AND VARIANCES OF THE FREQUENCY DISTRIBUTIONS OF THE SIZE
OF MATURITY AND SEX CLASSES BY CENSUS*

| | CENSUS | | | | |
|---|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| | 1932 (<i>N</i> = 23) | 1933 (<i>N</i> = 28) | 1935 (<i>N</i> = 15) | 1951 (<i>N</i> = 30) | 1959 (<i>N</i> = 44) |
| Males:† | | | | | |
| \hat{m}_0 | 2.52 | 2.80 | 3.12 | 0.38 | 3.18 |
| \bar{x} | 2.74 | 2.93 | 3.27 | 1.20 | 3.32 |
| s^2 | 1.84 | 1.40 | 2.78 | 0.17 | 3.11 |
| Females without young† | | | | | |
| \bar{x} | 4.70 | 3.36‡ | 4.47 | 3.30 | 6.14‡ |
| s^2 | 4.49 | 6.02 | 5.98 | 2.08 | 13.14 |
| Females with young† | | | | | |
| \bar{x} | 2.74 | 3.50 | 2.53 | 1.20 | 3.00 |
| s^2 | 1.66 | 4.26 | 1.41 | 1.27 | 4.70 |
| Infant 1: | | | | | |
| \bar{x} | 0.65 | 0.75 | 0.80 | 0.43 | 1.02 |
| s^2 | 0.51 | 0.42 | 0.60 | 0.60 | 1.42 |
| Infant 2: | | | | | |
| \bar{x} | 1.17 | 1.57 | 1.60 | 0.37 | 1.50 |
| s^2 | 0.79 | 1.88 | 0.54 | 0.38 | 2.30 |
| Infant 3: | | | | | |
| \bar{x} | 1.30 | 1.18 | 0.13 | 0.40 | 0.45 |
| s^2 | 2.04 | 1.93 | 0.12 | 0.32 | 0.58 |
| Juvenile 1: | | | | | |
| \bar{x} | 1.30 | 1.32 | 0.87 | 0.23 | 1.05 |
| s^2 | 1.22 | 0.89 | 0.98 | 0.19 | 1.30 |
| Juvenile 2: | | | | | |
| \bar{x} | 1.83 | 1.82 | 1.40 | 0.23 | 0.98 |
| s^2 | 2.06 | 1.19 | 1.40 | 0.19 | 1.51 |
| Juvenile 3: | | | | | |
| \bar{x} | 0.87 | 1.04 | 3.13 | 0.60 | 1.05 |
| s^2 | 1.21 | 1.29 | 2.12 | 0.46 | 1.16 |
| Mean troop size (= sum of means) | | | | | |
| | 17.30 | 17.46 | 18.20 | 7.97 | 18.50 |
| Variance of troop size | | | | | |
| | 49.95 | 48.33 | 51.03 | 12.72 | 88.07 |
| Sum of class variances | | | | | |
| | 15.82 | 19.28 | 15.93 | 5.56 | 29.22 |

* Males were compared with the O-truncated Poisson distribution; remaining classes were compared with the full Poisson.

† Tested against a fitted distribution and against a variance test; remaining classes were tested by variance test only.

‡ Fit to the Poisson distribution rejected at the .02 level by two-tailed truncated Poisson variance test, but full distribution acceptably fitted by theoretical truncated Poisson.

the size of that class (but rather on the birth rate of the adult females) and decreases (due to mortality or maturation into class "infant 2") at a rate which does depend on the size of the class.

Hence each sex and maturity class separately could be identified with a theoretical population behaving according to a BIDE process. The number of individuals in each such class should then be described by the BIDE process with immigration but no birth, that is, by the Poisson distribution. This argument applies to all of the maturity and sex classes because none of them contributes directly to its own increase (females with young do not give birth to other females with young). Since no troop was observed without an adult male, that class ought to be described by the truncated Poisson distribution.

Table 3 gives the means and variances of each maturity and sex class in each census and, for the adult males, the estimated parameter \hat{m}_0 . Theoretical distributions were fitted only to the adult classes. None of these fits was rejected by χ^2 in equation (7) at the .01 level. The Poisson variance test (equation [8]; truncated [equation (9)] for the males) was applied to each of the 45 distributions in table 3. As shown there, two of the distributions were rejected at the .02 level by a two-tailed test which rejected underdispersion at the .01 level and overdispersion at the .01 level. This is only one more rejection than would be expected if each distribution were known to be Poisson. Hence the assumption that the size of each maturity and sex class is (truncated) Poisson-distributed cannot be rejected.

Within each howler troop the sizes of the classes are not independent. If the class sizes were independent Poisson variates, then their sum (the troop size) would also be a Poisson variate whose variance equalled the sum of the class variances. The last two lines of table 3 show that for each census the sum of the class variances was much less than the variance of troop size. Where there is more of one class of howler, there is more of another.

GIBBONS

Counts of the sizes of troops of gibbons (genus *Hylobates*) have been made in northern Thailand by Carpenter (1940) and in the Malayan peninsula by Ellefson (1967). I am grateful to Dr. John O. Ellefson for permission to use here his previously unpublished data (given in Ellefson 1966, 1967). Table 4 summarizes Carpenter's counts of troops of *H. lar* and Ellefson's of *H. lar* and *H. agilis*. Each of these troops consists of a mother and father and a variable number of children. Both Carpenter and Ellefson reported seeing isolated males but excluded them from their data on troop size.

Since the number of individuals able to give birth in each troop is constant and equal to one, the troop size distribution ought to be predicted by the BIDE model with $\lambda = 0$ and ν positive, that is, by the (truncated) Poisson distribution. Further, since there is presumably no immigration to the troop once the parents have formed it, ν describes only the birth rate,

TABLE 4
FREQUENCY DISTRIBUTIONS OF SIZE OF GIBBON TROOPS*

| SIZE | CARPENTER | | ELLEFSON | |
|----------|---------------|---------------|---------------|------------------|
| | <i>H. lar</i> | <i>H. lar</i> | <i>H. lar</i> | <i>H. agilis</i> |
| 2..... | 2 | 6 | 4 | |
| 3..... | 1 | 14 | 2 | |
| 4..... | 8 | 4 | 2 | |
| 5..... | 6 | 3 | ... | |
| ≥ 6..... | 4 | 1 | ... | |

| Size | Observed <i>Hylobates lar</i> | Predicted <i>H. lar</i> | Observed Total | Predicted Total |
|----------|----------------------------------|----------------------------|-------------------|--------------------|
| 2..... | 8 | 10.9 | 12 | 14.4 |
| 3..... | 15 | 12.5 | 17 | 15.3 |
| 4..... | 12 | 10.7 | 14 | 12.2 |
| 5..... | 9 | 7.3 | 9 | 7.8 |
| ≥ 6..... | 5 | 7.6 | 5 | 7.2 |

| | | |
|-------------------|----------|----------|
| \hat{m}_1 | 3.429 | 3.193 |
| X^2 | 2.732 | 1.689 |
| df | 3 | 3 |
| P | (.3, .5) | (.5, .7) |

* Data are from Carpenter (1940) and Ellefson (1967). Unpublished data reproduced by kind permission of Dr. John O. Ellefson.

not the sum of birth plus (troop) immigration rates. Because troops of size 1 are excluded, the observed data should be fitted by the 0,1-truncated Poisson distribution.

Table 4 shows that the 0,1-truncated Poisson distribution does describe satisfactorily the sum of Ellefson's and Carpenter's data on *H. lar* and the sum of the data on *H. lar* and *H. agilis*. Though the pooling of data on two different species seems biologically questionable a priori, both Carpenter and Ellefson emphasize the behavioral unity of these gibbons and the similarity in size and shape. As shown, the results of testing the pooled data support that asserted unity.

The estimate that the ratio of the mean rate of births per troop per year to the mean rate per individual of death or emigration per year is approximately 2.8 again needs to be checked independently.

COLOBUS AND LANGURS

Marler (1969) reported the size and composition of 19 troops of black and white colobus monkeys (*Colobus guereza*) he observed in Uganda, along with the sizes of five troops reported by previous observers (table 5).

Although the data are too few by themselves to make a convincing case for the accuracy of the BIDE model's equilibrium distribution, they fall into the pattern being presented.

The 14 troop sizes Marler observed in the Budongo Forest, Uganda, are consistent with a truncated Poisson distribution. The truncated Poisson variance test (equation [9]) gives $X^2 = 17.170$ with 13 degrees of freedom.

TABLE 5
FREQUENCY DISTRIBUTIONS OF SIZE OF COLOBUS TROOPS*

| I Size | II Budongo | III Pred. | IV Q. Eliz. | V Other | VI Total | VII Poisson | VIII Neg. bin. |
|-------------------|---------------|--------------|----------------|------------|-------------|----------------|-------------------|
| 1..... | ... | 1.1 | 1 | ... | 1 | 2.2 | 1.0 |
| 2..... | 1 | | ... | ... | 1 | | |
| 3..... | ... | | 1 | ... | 1 | | |
| 4..... | 1 | 1.1 | ... | ... | 1 | 2.1 | 1.3 |
| 5..... | 1 | | 1 | ... | 2 | | |
| 6..... | 1 | 1.6 | ... | 2 | 3 | 2.8 | 2.6 |
| 7..... | 1 | 1.9 | ... | ... | 1 | 3.3 | 2.6 |
| 8..... | 2 | 1.9 | 1 | ... | 3 | 3.3 | 2.5 |
| 9..... | 2 | 1.8 | 1 | ... | 3 | 3.0 | 2.2 |
| 10..... | ... | 1.5 | ... | 1 | 3 | 2.5 | 1.9 |
| 11..... | 3 | 1.1 | ... | ... | ... | 1.8 | 1.5 |
| 12..... | ... | 2.0 | ... | 1 | 1 | 1.2 | 1.2 |
| 13..... | 2 | | ... | ... | ... | 1.7 | 1.6 |
| 14..... | ... | | ... | ... | ... | | |
| ≥ 15..... | ... | | | | | | 1.5 |
| \bar{X}^2 | | 5.820 | ... | ... | ... | 9.531 | 7.693 |
| df..... | | 7 | ... | ... | 3 | 8 | 10 |
| P..... | | (.5, .7) | ... | 1 | 1 | (.2, .3) | (.5, .7) |

* Data are from Marler (1969). I: Size of colobus troop. II: Marler's observations in Budongo Forest, Uganda. III: Truncated Poisson distribution fitted to II; $\hat{m}_0 = 8.357$. IV: Marler's observations in Queen Elizabeth National Park, Uganda. V: Observations of Ullrich, and Schenkel and Schenkel-Hulliger, as reported by Marler (1969). VI: Sum of II, IV, V; all observations. VII: Truncated Poisson distribution fitted to VI; $\hat{m}_0 = 8.132$. VIII: Truncated negative binomial distribution fitted to VI; $\hat{p} = 0.548, \hat{r} = 9.770$.

TABLE 6
FREQUENCY DISTRIBUTION OF SIZE OF BISEXUAL TROOPS OF HANUMAN LANGURS*

| Size | Observed | Predicted |
|-----------|-------------------|-------------|
| 1-7..... | 0 | 1.3 |
| 8..... | 0 | 1.0 |
| 9..... | 2 | 1.5 |
| 10..... | 3 | 2.0 |
| 11..... | 7 | 2.5 |
| 12..... | 5 | 2.9 |
| 13..... | 1 | 3.2 |
| 14..... | 1 | 3.4 |
| 15..... | 2 | 3.3 |
| 16..... | 2 | 3.1 |
| 17..... | 3 | 2.8 |
| 18..... | 1 | 2.5 |
| 19..... | 3 | 2.1 |
| 20..... | 1 | 1.7 |
| 21..... | 3 | 1.3 |
| 22..... | 1 | 1.7 |
| 23..... | 2 | |
| ≥ 24..... | 1 | 1.6 |
| | \hat{p} | 0.727 |
| | \hat{r} | 40.251 |
| | \bar{X}^2 | 21.379 |
| | df..... | 14 |
| | P..... | (0.05, 0.1) |

* Data are from Sugiyama (1964).

The probability of a larger value by chance lies between .1 and .2. A distribution fitted to these data in table 5 is acceptable with higher probability, as expected, because of the small number of observations.

The total 24 observations reported by Marler may also be acceptably fitted by a truncated Poisson distribution, as shown in table 5. But the truncated Poisson variance test (equation [9]) gives $X^2 = 40.3$ with 23 degrees of freedom. The probability of a larger value by chance lies between .01 and .02; so the acceptability of the truncated Poisson distribution is doubtful.

As also shown in table 5, a truncated negative binomial distribution fits substantially better. This negative binomial distribution may be the result of pooling Poisson distributions with different means in different localities, and not the result of a positive per-individual birth rate. Further data from each locality are required to clarify how the negative binomial actually arises.

Sugiyama (1964) did a roadside survey of the sizes of troops of hanuman langurs (*Presbytis entellus*) near Dharwar, India. He emphasized the difficulty of obtaining accurate counts. His best data, on the sizes of 38 bisexual troops (Sugiyama 1964, p. 17) appear in table 6, along with a fitted truncated negative binomial distribution. The fit is just barely acceptable at the 5 percent level when 14 degrees of freedom are assigned. When 16 degrees of freedom are assigned, $.1 < P < .2$. Like the data on colobus, these langur observations are too few to make a convincing case for or against any distribution. At least they are consistent with the general pattern.

BABOONS

Table 7 summarizes the size of troops of three species of baboons observed in several localities by Warshall, Washburn, DeVore, Hall, and the Altmanns (DeVore and Hall 1965, p. 29; Altmann and Altmann, in press). I thank Dr. Stuart A. Altmann and Mr. Peter J. Warshall for permission to use here previously unpublished data.¹

DeVore and Hall reported their size counts grouped into the intervals 1-9, 10-19, 20-29, . . . ; Altmann reported his size counts grouped into the intervals 1-10, 11-20, 21-30, To describe both systems I have adopted the overlapping set of intervals 1-10, 10-20, 20-30, . . . and in the following calculations have assumed that the frequency within each interval falls at its midpoint, 5, 15, 25, The effect on the variance of this assumption will be neglected.

Hall observed the sizes of 53 troops of chacma baboons (*Papio ursinus*) in three separate areas of southern Africa. DeVore and Hall present only

¹ Altmann has privately observed that different compilations of Hall's observations of chacma baboons differ from each other and from the original publication. These data will be clarified and presented along with additional data of other observers in the monograph of Altmann and Altmann (in press).

the pooled frequencies, and it is assumed here that the birth, immigration, and loss rates are the same for all troops included in the observed distribution. The predicted truncated negative binomial distribution agrees well with the observed, as shown in table 7.

According to the estimated parameters, the ratio of the mean number of immigrants per year to the mean number of births per individual per year is approximately 2.7. The ratio of birth rate to loss rate is approximately 0.93. The evidence that immigration takes place is two observations of adult males who shifted from one troop to another (location unspecified; DeVore and Hall 1965, p. 38). But it is not possible with the available data to make quantitative estimates of immigration, birth, or loss rates independently.

Altmann observed 48 troops, Washburn observed 15 troops, and Warshall observed 16 troops of yellow baboons (*Papio cynocephalus*) in Amboseli Reserve, Kenya. In pooling Warshall's original data into intervals for table 7, I used Altmann's system. As shown, Altmann's observations alone may be described by the truncated negative binomial distribution. The fit remains acceptable when Altmann's, Washburn's, and Warshall's observations are combined. The remark made above about the possible dependence of successive censuses of howler monkeys applies here, especially since Altmann's and Warshall's counts were made within one year. The fit to the combined frequency distribution is at least as good as the probability level indicates.

Pooling all the observed sizes of baboon troops gives the total distribution in table 7 (column XIV). The fit of the truncated negative binomial distribution is marginal or poor. That the fit to the total distribution is clearly worse than the fit to each separate species, distribution suggests at least that the parameters of the different species are different.

A LOOK AT DYNAMICS

In all of these primate studies the only possibility of checking the detailed dynamics of the BIDE model by getting independent estimates of the parameters is provided by a few data of Altmann and Altmann (in press). These data demonstrate clearly the virtue and necessity of sustained, detailed, quantitative observation and reporting of primates.

Table 8, from Altmann, describes the changes in population size of Altmann's main study troop during a year of observation. The numbers in the table, starting from row 1 at the top, are to be interpreted as follows: The troop, when first observed, had 40 members. After 41 days at that size, a birth occurred, raising the troop size to 41. After 5 days at that size, a birth again increased troop size to 42; and so on.

From table 8 it is easy to construct a frequency histogram of the number of days between births and another frequency histogram of the number of days between losses (deaths or emigrations). The BIDE model would predict that both of these histograms would have a negative exponential shape, with scale parameters λ and μ , respectively. Though the data are too

TABLE 7
FREQUENCY DISTRIBUTIONS OF SIZE OF BABOON TROOPS*

| I Size | II Hall | III Pred. | IV Alt- mann | V Pred. | VI Wash- burn | VII War- shall | VIII Yellow | IX Pred. | X DeVore | XI War- shall | XII Olive | XIII Pred. | XIV Total | XV Pred. |
|--------------|------------|--------------|--------------------|------------|---------------------|----------------------|----------------|-------------|-------------|---------------------|--------------|---------------|--------------|-------------|
| 1-10 | 1 | 3.9 | ... | 1.7 | ... | 1 | 1 | 3.2 | ... | ... | ... | 3.1 | 2 | 10.2 |
| 10-20 | 12 | 10.2 | 2 | 5.3 | 1 | 2 | 5 | 8.1 | 2 | ... | 2 | ... | 19 | 21.0 |
| 20-30 | 16 | 11.3 | 11 | 7.5 | ... | 3 | 14 | 10.6 | 3 | ... | 6 | 3.5 | 36 | 24.1 |
| 30-40 | 9 | 9.4 | 10 | 7.9 | ... | 2 | 12 | 11.1 | ... | 3 | 3 | 3.5 | 24 | 22.6 |
| 40-50 | 4 | 6.8 | 7 | 7.2 | 2 | 3 | 12 | 10.3 | 1 | 1 | 2 | 2.8 | 18 | 19.1 |
| 50-60 | 6 | 4.5 | 7 | 5.9 | 2 | 1 | 10 | 8.8 | ... | ... | ... | 2.0 | 16 | 15.2 |
| 60-70 | 1 | 2.8 | 4 | 4.6 | 2 | ... | 6 | 7.3 | 1 | 1 | 2 | 1.3 | 9 | 11.6 |
| 70-80 | 1 | 1.7 | 3 | 3.4 | 3 | 1 | 7 | 5.8 | 1 | 1 | 2 | 1.8 | 10 | 8.6 |
| 80-90 | 1 | 2.3 | 5 | 2.4 | 1 | 1 | 7 | 4.5 | 1 | ... | 1 | ... | 9 | 6.3 |
| 90-100 | ... | ... | ... | 1.7 | 1 | 1 | 2 | 3.4 | ... | ... | ... | ... | 2 | 4.5 |
| 100-110 | 2 | ... | 1 | 1.2 | 1 | ... | 2 | 2.5 | ... | ... | ... | ... | 4 | 3.1 |
| 110-120 | ... | ... | ... | ... | ... | ... | ... | 1.8 | ... | ... | ... | ... | ... | 2.2 |
| 120-130 | ... | ... | ... | ... | ... | ... | ... | 1.3 | ... | ... | ... | ... | ... | 1.5 |
| 130-140 | ... | ... | ... | ... | ... | ... | ... | 1.6 | ... | ... | ... | ... | ... | 1.0 |
| 140-150 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 150-160 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 160-170 | ... | ... | ... | 2.2 | 1 | 1 | 1 | ... | ... | ... | ... | ... | 1 | 2.1 |
| 170-180 | ... | ... | ... | ... | 1 | ... | 1 | 1.6 | ... | ... | ... | ... | 1 | ... |
| 180-190 | ... | ... | ... | ... | 1 | ... | 1 | ... | ... | ... | ... | ... | 1 | ... |
| 190-... | ... | ... | 1 | ... | ... | ... | 1 | ... | ... | ... | ... | ... | 1 | ... |
| $\hat{\rho}$ | ... | 0.0727 | ... | 0.0560 | ... | ... | ... | 0.0435 | ... | ... | ... | 0.0829 | ... | 0.0470 |
| \hat{r} | ... | 2.729 | ... | 2.986 | ... | ... | ... | 2.518 | ... | ... | ... | 3.717 | ... | 2.296 |
| χ^2 | ... | 7.827 | ... | 11.381 | ... | ... | ... | 15.905 | ... | ... | ... | 5.495 | ... | 22.961 |
| df | ... | 6 | ... | 9 | ... | ... | ... | 12 | ... | ... | ... | 4 | ... | 12 |
| P | ... | (.2, .3) | ... | (.2, .3) | ... | ... | ... | (.2, .3) | ... | ... | ... | (.2, .3) | ... | (.02, .05) |

* Data are from DeVore and Hall (1965), Altmann and Altmann (in press), and Warshall (unpublished). Unpublished data reproduced by kind permission of Dr. Stuart A. Altmann and Mr. Peter J. Warshall. I: Size of baboon troops; for choice of intervals, see text. II: Hall's observations of chacma baboons, southern Africa. III: Truncated negative binomial distribution fitted to II. IV: Altmann's observations of yellow baboons in Amboseli, Kenya. V: Truncated negative binomial distribution fitted to IV. VI: Warshall's observations of yellow baboons in Amboseli, Kenya. VII: Warshall's observations of yellow baboons in Amboseli, Kenya (July 1964). VIII: Sum of IV, VI, and VII (all yellow baboons). IX: Truncated negative binomial distribution fitted to VII. X: DeVore's observations of olive baboons, Nairobi Park, Kenya. XI: Warshall's observations of olive baboons, Nairobi Park, Kenya (1964). XII: Sum of X and XI (all olive baboons). XIII: Truncated negative binomial distribution fitted to XII. XIV: Sum of II, VIII, XII (all baboons). XV: Truncated negative binomial distribution fitted to XIV. With 14 df, .05 < P < .10.

TABLE 8
 BIRTH (B), IMMIGRATION (I), DEATH (D), AND EMIGRATION (E)
 IN ALTMANN'S MAIN STUDY TROOP*

| Row <i>j</i> | After this many days | at this troop size | this event occurred. |
|-----------------|-------------------------|-----------------------|-------------------------|
| 1 | 41 | 40 | B |
| 2 | 5 | 41 | B |
| 3 | 22 | 42 | B |
| 4 | 2 | 43 | D |
| 5 | 17 | 42 | D |
| 6 | 26 | 41 | I |
| 7 | 0 | 42 | I |
| 8 | 55 | 43 | B |
| 9 | 35 | 44 | I |
| 10 | 20 | 45 | E |
| 11 | 5 | 44 | D |
| 12 | 6 | 43 | E |
| 13 | 32 | 42 | D |
| 14 | 4 | 41 | D |
| 15 | 0 | 40 | D |
| 16 | 22 | 39 | D |
| 17 | 10 | 38 | B |
| 18 | 0 | 39 | B |
| 19 | 7 | 40 | D |
| 20 | 4 | 39 | B |
| 21 | 17 | 40 | D |
| 22 | 11 | 39 | E |
| 23 | 3 | 38 | B |
| 24 | 4 | 39 | D |
| 25 | 8 | 38 | D |
| 26 | 2 | 37 | D |
| 27 | 5 | 36 | B |
| 28 | 10 | 37 | B |
| | final | 38 | ... |

* Unpublished data reproduced by kind permission of Dr. Stuart A. Altmann. For further explanation see text.

few to confirm this prediction in detail, the actual histograms (not shown) do have an approximately negative exponential shape, being highest near the origin and asymptoting concavely to zero.

To obtain estimates of λ , μ , and ν from table 8, let T_j be the number of days in the j th row and let X_j be the size in the j th row which the troop maintained for T_j days. Then simply summing up the number of monkey-days at risk of giving birth or of leaving the troop, we have

$$\text{expected births} = \lambda \sum_{j=1}^{28} T_j X_j = \lambda(15407) \quad (10)$$

and

$$\text{expected losses} = \mu \sum_{j=1}^{28} T_j X_j = \mu(15407), \quad (11)$$

where λ and μ are in units of individual⁻¹ day⁻¹. Since the probability of immigration to the troop is assumed independent of troop size, we also have

$$\text{expected immigrations} = v \sum_{j=1}^{28} T_j = v \cdot 373, \tag{12}$$

where v is in units of day^{-1} .

Setting the expected numbers of births, losses, and immigrations equal, respectively, to the numbers actually observed, namely, 10, 15, and 3, gives the estimates $\lambda = 0.000649$ per individual per day, $\mu = 0.000974$ per individual per day, and $v = 0.008043$ per day. Note that the initial assumption that $\lambda < \mu$ is here independently confirmed. In view of the small numbers of observed events on which these estimates are based, no confidence should be attached to the significant figures after the first; but it seemed best to postpone rounding until after the calculations based on these estimates were complete. The "jackknife," an extremely powerful statistical technique to be described and used in the Appendix, will make it possible to set confidence limits around these estimates of λ , μ , and v .

From equation (2) the parameters of the truncated negative binomial distribution estimated from table 8 are $r = 12.392$ and $q = 0.667$. Ideally, the next step would be to compare a truncated negative binomial distribution having these parameters with the frequency distribution of size of the main study troop on which the parameters are based.

From table 8 it is possible to construct a frequency distribution showing the number of days the troop was at each size. But because of the low rates of change in troop size per day, the period of observation was too short for the full variability of troop size to appear. (Analogously, if a stock price is watched for only a week, it is not possible to estimate the full distribution of the price because there has not been time enough for it to vary.) Instead, it is necessary to fall back on the assumption that all the other troops of yellow baboons observed in Amboseli are independent replicates of the same BIDE process.

Table 9 shows the result of comparing the predictions using these parameters with Altmann's observations and with all observations of Amboseli

TABLE 9
FREQUENCY DISTRIBUTIONS OF SIZES OF YELLOW BABOON TROOPS COMPARED WITH TRUNCATED NEGATIVE BINOMIAL DISTRIBUTIONS*

| SIZE | I ALTMANN ONLY | | II ALL AMBOSELI | |
|-------------------|-------------------|-----------|--------------------|-----------|
| | Observed | Predicted | Observed | Predicted |
| 1-10 | ... | 1.4 | 1 | 2.2 |
| 10-20 | 2 | 16.0 | 5 | 25.7 |
| 20-30 | 11 | 21.8 | 14 | 35.1 |
| 30-40 | 10 | 9.4 | 12 | 15.2 |
| 40- | 28 | 2.4 | 50 | 3.8 |
| \bar{X}^2 | 297.15 | | 592.46 | |
| df | 2 or 4 | | 2 or 4 | |
| P | <<.01 | | <<.01 | |

* Parameter values calculated from table 8, $p = 0.333$, $r = 12.4$. I: Altmann's observations only. II: All yellow baboon counts in Amboseli.

yellow baboons combined. The fits are clearly unacceptable, whether the X^2 statistic is given two or four degrees of freedom.

Sustained observation of the main study troop and repeated censuses of all troops in Amboseli Reserve over a period of several years could show whether this failure is due to (1) small-sample fluctuations in the present estimates of the parameters, (2) a difference in parameters between the main study troop and the other troops in the reserve, or (3) the failure of the BIDE process to represent accurately the dynamics of growth and loss in this primate troop.

To rule out the first possibility, of small-sample fluctuations, it would be necessary to show a greater difference than could be accounted for by chance alone between the parameters of a truncated negative binomial distribution obtained by fitting the distribution of troop size and the parameters obtained from vital statistics (table 8). For example, for Altmann's baboons, from table 7, column V, p (fitted) = 0.056, r (fitted) = 2.986. We have just found p (vital) = 0.333, r (vital) = 12.392. Thus p (fitted) - p (vital) \equiv $\text{diff}(p)$ = -0.277, and r (fitted) - r (vital) \equiv $\text{diff}(r)$ = -9.406. Given an estimate of the variance of $\text{diff}(p)$ and the variance of $\text{diff}(r)$, we could construct 95 percent confidence intervals around $\text{diff}(p)$ and $\text{diff}(r)$. If zero fell within these confidence intervals, then we could conclude that the fitted parameters and those based on vital statistics did not differ at the 5 percent level, and hence that, within the fineness of detail of the available data, the baboon's population dynamics were consistent with the BIDE model.

The Appendix describes and applies to this question a very general, powerful statistical technique called the "jackknife." Though this technique of estimating variability in limited samples of data has existed for over a decade, I do not know of previous applications in biology.

The conclusion obtained from using the jackknife is that $\text{diff}(p)$ is significantly different from zero at the 5 percent level, while $\text{diff}(r)$ is not; hence the parameter estimates of at least p based on fitting and on vital statistics are probably different. See the Appendix for details.

The second possible explanation of the discrepancy between observed and predicted counts in table 9, namely, a difference in parameters between the main study troop and the other troops in the reserve, can only be established by further field observations.

If, as is more likely, the BIDE process fails to represent accurately the dynamics of growth and loss in this primate troop, then theoretical probabilists will be called upon to construct more realistic stochastic models consistent with the main finding of this paper: that the equilibrium distributions of troop sizes in a wide variety of free-ranging primates are described by the truncated negative binomial or truncated Poisson distributions. The simple birth-immigration-death-emigration model presented here will then have served its purpose by directing attention to this regularity and providing a first-order explanation of it.

FURTHER PROBLEMS

These results suggest many more investigations. Possibilities lie (1) within the purview of the BIDE model, (2) in ecology, (3) in population genetics, and (4) in more systematic data and more realistic stochastic population models.

First, in the BIDE model, if the birth rate remains constant but the immigration rate approaches zero so that there is just enough immigration to restart a theoretical population that becomes extinct, then the population size will be logarithmically distributed (Bailey 1964, p. 100). This mathematical result constitutes a challenge to field biologists to find a collection of primate troops living in similar habitats but so separated that almost no exchange between troops (no immigration) occurs. These troops should also not have a birth rate that is independent of troop size, as it is in the gibbons. The BIDE model then predicts that troop sizes will be logarithmically distributed.

Second, the above results do not explain the parameters of the distributions of troop size. Why, for example, are there not half as many howler troops, each twice as large, on Barro Colorado Island? Japanese macaques may illuminate the effects both of different habitats on the same species (since Japanese macaques occur naturally over a substantial range of latitudes) and of sudden great increases in the production of the environment; the practice of feeding the macaque troops, initiated by the Japanese scientists in order to facilitate behavioral observations, may be the simian equivalent of an agricultural revolution. Analysis of the demographic consequences might suggest how and what ecological factors influence population parameters (cf. Kawai, Azuma, and Yoshida 1967).

Third, theories of population dynamics and population genetics remain to be wedded. In classical population genetics, the theoretical study of populations subdivided into groups each of which forms more or less a breeding unit by itself (Li 1955, chap. 21) has generally assumed that each group contains the same number of breeding individuals. But the breeding units (troops) of the primates described here vary in size. Certain results such as Wahlund's formula are easily extended to groups of variable size within a theoretical population. Other effects of great importance, such as inbreeding, migration, and selection, have not yet been examined when group size is Poisson or negative binomially distributed. For such genetic and other analysis, one needs stochastic models of systems of groups (in the present cases, troops) which are not independent—in which, for example, the emigrants from some groups become the pool of immigrants for other groups. Such models have been constructed for population sizes (Puri 1968) and for sociological applications (Cohen, "Casual Groups of Monkeys and Men: Stochastic Models of Elemental Social Systems," in prep.), but the genetics is largely unexplored (Pollak 1968).

Finally, insufficient interaction between model builders and field bio-

logists usually leaves biologists indifferent to unrealistic models and leaves modelers hungry for systematic data to test the details of models. Field biologists might find realistic questions for which their data would be useful in recent developments in multidimensional linear birth-and-death processes (Milch 1968), which describe theoretically the fluctuations in populations containing different genotypes. Available data might prompt modelers to ask: what other, more realistic stochastic population models can represent the known differences in natality, mortality, and migration due to maturity and sex (Goodman 1968), the seasonality of birth, the effects of social status within the troop on breeding, and possibly other data, and still tie together in a predictive way all the data on troop size presented here? Can such a model be constructed which is also analytically tractable?

SUMMARY

A simple stochastic population model which assumes constant birth, loss (death or emigration), and immigration rates equally and independently applicable to all individuals in a theoretical population predicts at equilibrium a negative binomial distribution of population size if all three rates are strictly positive and a Poisson distribution of population size if only the birth rate is zero or if births occur at a rate independent of population size.

If the theoretical population of the model is interpreted as a troop of free-ranging primates (and not necessarily as a genetic or ecological population), several species of primates appear to confirm the equilibrium predictions of the model.

The observed frequency distributions of size of troops of howler monkeys approximate a truncated negative binomial except after an epidemic which removed young monkeys; the size distribution, then, is nearly truncated Poisson, as expected.

In gibbons, whose troops have a birth rate independent of troop size, the observed distributions appear to be truncated Poisson. Though few data are available, colobus monkeys seem consistent with this pattern.

Sizes of bisexual troops of hanuman langurs approximate a truncated negative binomial distribution. Baboon troops have approximately truncated negative binomial distributions of size, but the parameters of the distributions appear to differ more from one species to another than to the parameters of the distributions fitted to different gibbon species.

The only available detailed vital statistics on a single baboon troop suggest that the simple dynamics of the stochastic model is not faithful to what actually happens, even though the equilibrium distributions are. A statistical technique apparently new to biology, called the "jackknife," indicates that the variability of the baboon data is not sufficient to account for the difference between the estimate of a parameter of the truncated negative binomial obtained by fitting the troop size distribution and the estimate of the same parameter obtained from vital statistics. Hence the innards of the model may be faulty. Both better models and better data, especially in combination, are needed.

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APPENDIX

THE JACKKNIFE AND ITS APPLICATION

"The jackknife offers ways to set sensible confidence limits in complex situations," say Mosteller and Tukey (1968, p. 134). The bare bones of the technique, as they present it, along with my way of applying it to Altmann's baboon data, will be presented here.

The goal is to assess the variance of any statistic y (such as r [fitted] or r [vital] or $\text{diff}[r]$) with respect to a given sample of data (such as table 7, column IV; and table 8). Suppose the sample is divided into some number k of blocks of observations. Let $y_{(j)}$ be the value of the statistic obtained on the basis of all observations in the sample except those in the j th block, that is, with the j th block omitted. Let y_{all} be the statistic calculated on the basis of the whole sample. Then pseudovalues are defined as

$$y_{*j} = ky_{\text{all}} - (k-1)y_{(j)}, \quad j = 1, 2, \dots, k. \quad (\text{A-1})$$

The jackknifed estimate, the "best single result," is then given by

$$y_* = (y_{*1} + \dots + y_{*k})/k; \quad (\text{A-2})$$

and an estimate of its variance is given by

$$s_*^2 = [\sum y_{*j}^2 - (\sum y_{*j})^2/k]/[k(k-1)]. \quad (\text{A-3})$$

Mosteller and Tukey (1968, pp. 136-138) adjoin various admonitions to this simple calculation, admonitions which have been heeded but will not be repeated here. According to their rule of thumb, the degrees of freedom for the value of t used to find the confidence interval are one less than the number of different numbers which appear as pseudovalues.

To apply the jackknife to the fitted parameters p (fitted) and r (fitted) as given by equation (6), I found from tables a random permutation of the integers from 1 to 51 (Altmann observed 51 troops). Ranking the observed troop sizes from smallest to largest, I then crossed off the five observations whose rank was given by the first five random numbers. On the basis of the remaining 46 observations, I calculated $p_{(1)}$ and $r_{(1)}$ from equation (6), the subscript indicating that the first block was omitted. I then restored those five observations and struck out the next five randomly ranked observations to obtain $p_{(2)}$ and $r_{(2)}$. The last estimates, $p_{(10)}$ and $r_{(10)}$, were based on the 45 observations remaining when the last six randomly ranked observations were struck out. In this way each observation was omitted from just one estimate of $p_{(j)}$ and $r_{(j)}$.

Pseudovalues were found from equation (A-1) by replacing y first by p and then by r . Jackknifed estimates p_* and r_* and their variances $s_*^2(p)$ and $s_*^2(r)$ then follow from equations (A-2) and (A-3).

The first two lines of table A1 show that the resulting jackknifed estimate of p (fitted) is 0.0770 and that the standard deviation (square root of variance) of that estimate is 0.00476. (All calculations were carried out to eight significant figures; only the first few are reported here.) Since this variance has nine degrees

TABLE A1
RESULTS OF APPLYING THE JACKKNIFE TO THE PARAMETERS OF THE
BIDE MODEL ESTIMATED FROM DATA OF ALTMANN*

| Parameter | y_* | s_* | df | 95% confidence |
|------------------------|-----------------------|----------------------|----|------------------------------|
| p (fitted) | 0.077 | 0.00476 | 9 | (.066,.088) |
| r (fitted) | 3.988 | 0.437 | 9 | (3.00,4.98) |
| p (vital) | 0.328 | 0.0370 | 9 | (.245,.412) |
| r (vital) | 7.843 | 12.461 | 9 | (-20.3,36.0) |
| diff (p) | -0.252 | 0.036 | 9 | (-.333,-.170) |
| diff (r) | -3.855 | 12.486 | 9 | (-32.1,24.4) |
| λ | 6.5×10^{-4} | 2.9×10^{-4} | 9 | $(-0.2,13.1) \times 10^{-4}$ |
| μ | 16.1×10^{-4} | 8.7×10^{-4} | 9 | $(-3.5,35.8) \times 10^{-4}$ |
| ν | 8.0×10^{-3} | 5.7×10^{-3} | 9 | $(-4.9,21.0) \times 10^{-3}$ |

* Altmann's data: from table 7, col. IV; and table 8. y_* = the jackknifed estimate of the parameter value; s_* = its standard deviation; df = the degrees of freedom used to construct the 95% confidence interval.

of freedom, the 95 percent confidence interval is $p_* \pm |t_{9|.95} \cdot s_*$ (p) = $0.077 \pm (2.262)(0.00476) = (0.066, 0.088)$, as shown in the first line of table A1. The confidence intervals in the remaining lines are calculated in the same way.

To apply the jackknife to the estimates of p and r based upon the vital statistics, I divided the sequence of 373 days recorded in table 8 into 10 blocks, the first, fifth, and tenth containing 38 days and the remaining blocks containing 37. In sequence, block by block, I removed each set of days and the events which occurred during those days from table 8 and calculated the parameters $\lambda_{(j)}$, $\mu_{(j)}$, and $\nu_{(j)}$ from equations (10), (11), and (12) and the parameters $r_{(j)}$ and $p_{(j)}$ from equation (2). For example, when the first 38 days are omitted, 335 days remain; during that time there were 10 births, 3 immigrations, and 15 losses. When the last 38 days are omitted, in the remaining 335 days there were 7 births, 3 immigrations, and 11 losses.

The results of applying the jackknife to λ , μ , and ν and to p (vital) and r (vital) appear in table A1. The negative values for the lower ends of the confidence intervals around r (vital), λ , μ , and ν are an artifact of the jackknife, which approximates the distribution of a statistic by a symmetrical distribution. For purposes of interpretation, these negative lower limits should be adjusted upward to zero. Mosteller and Tukey (1968) suggest other ways of getting around this problem.

To apply the jackknife to $\text{diff}(p) = p$ (fitted) - p (vital) and $\text{diff}(r) = r$ (fitted) - r (vital), block estimates were formed by simple subtraction: $\text{diff}(p)_{(j)} = p_{(j)}$ (fitted) - $p_{(j)}$ (vital) (similarly for r); and equations (A-1), (A-2), and (A-3) were applied. The results are given in table A1. While the estimate of r based on fitting the equilibrium distribution does not differ significantly at the 5 percent level from the estimate of r based on the vital statistics, the two estimates of p do differ significantly.

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