Markov Population Processes as Models of Primate Social and Population Dynamics

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Thanks to recently developed theory of Markov population processes, models of how an individual primate migrates from one casual social group to another or from one breeding troop to another can now deal exactly with transition rates which depend nonlinearly on the sizes of both the group (or troop) left and the group (or troop) entered. Examples of such models presented here are consistent with existing observations of primate social and population dynamics and are more plausible as explanations of these data than previous linear models.

1. INTRODUCTION

A Markov population process (Kingman 1969) is a stochastic population process defined on k-tuples of nonnegative integers. Individuals arrive at, depart from, and transfer among the k positions. The number of individuals at any instant in each position is given by the corresponding integer in the k-tuple which describes the system at that instant. Theorems permit calculation, in some special cases, of the stationary distributions of the numbers of individuals at each position from the instantaneous rates of arrival, departure, and transfer (Section 2). Two sets of such rates, describing systems with a variable number of individuals, lead to negative binomial marginal distributions of the number of individuals at each position. A third set of rates, describing a system with a fixed number of individuals, leads to a marginal distribution of the number of individuals per position that is negative binomial only in the limit as the number of individuals and positions in the system is large (Section 3). Calculation of aggregate rates of arrivals to and departures from groups of each size shows that these rates are linear functions of group size in the two models of open systems, are quadratic functions in the model of a closed system, and in all cases are consistent with the marginal distributions of group size (Section 4).

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The three new Markov population processes presented here improve on previous linear one-step transition (LOST) models for systems of freely forming social groups because the nonlinear models do away with the need for certain implausible assumptions in interpreting the equations of the LOST models (Section 5). The Markov population process models also improve on previous birth-immigration–death-emigration (BIDE) models which treat ensembles of primate troops (breeding units) as independent, noninteracting replicates of a BIDE process; by their very multidimensionality, Markov population processes allow for the possibility and suggest the measurement of intertroop migration and other demographic interaction (Section 6). Several other recent multidimensional stochastic models, though not immediately applicable to primates, are special cases of or closely related to Markov population processes (Section 7).

2. MARKOV POPULATION PROCESSES

Following Kingman (1969: 1–4), let k be any positive integer and let $\mathbf{n} = (n_1, ..., n_k)$ and $\mathbf{m} = (m_1, ..., m_k)$ be k-vectors whose components n_i and m_i are nonnegative integers. We define a continuous-time Markov chain on some subset S of the set of all such vectors, and denote by $q(\mathbf{n}, \mathbf{m})$ the transition rate (not to be confused with the transition probability) from $\mathbf{n}$ to $\mathbf{m}$. Write $\mathbf{e}_i$ for the vector with all components zero except for 1 in the ith place. Then the transition from $\mathbf{n}$ to $\mathbf{n} + \mathbf{e}_i$ may be described as an arrival at component i; the transition from $\mathbf{n}$ to $\mathbf{n} - \mathbf{e}_i$ as a departure from i; and the transition from $\mathbf{n}$ to $\mathbf{n} - \mathbf{e}_i + \mathbf{e}_j$ as a transfer from i to j, $i \neq j$ (assuming $k \geqslant 2$). A continuous-time Markov chain on S is a Markov population process if and only if, for any $\mathbf{n}$, $q(\mathbf{n}, \mathbf{m}) = 0$ except possibly for

$$q(\mathbf{n}, \mathbf{n} + \mathbf{e}_i) = \alpha_i(\mathbf{n})$$

$$q(\mathbf{n}, \mathbf{n} - \mathbf{e}_i) = \beta_i(\mathbf{n}), \tag{1}$$

$$q(\mathbf{n}, \mathbf{n} - \mathbf{e}_i + \mathbf{e}_j) = \gamma_{ij}(\mathbf{n}) \qquad (i \neq j).$$

The boundary conditions on these transitions are $\beta_i(\mathbf{n}) = \gamma_{ij}(\mathbf{n}) = 0$ if $n_i = 0$.

For present applications it is assumed that the Markov chain on S is irreducible. A Markov population process on S is closed if $\alpha_i = \beta_i = 0$ for all i (no arrivals or departures) so that the number of individuals in the system $n = n_1 + \cdots + n_k$ is conserved. In this case S is the set of vectors whose components sum to n. In an open system, $S = \{\mathbf{n} \mid n_1 \leqslant L_1, ..., n_k \leqslant L_k\}$ where $\mathbf{L}$ is a vector of upper limits some or all of whose components L_i may be infinite. Processes with absorbing states are not considered here.

The stationary distribution on S is a set of positive numbers $p(\mathbf{n})$, for $\mathbf{n}$ in S, satisfying

$$\sum_{\mathbf{n} \in S} p(\mathbf{n}) = 1 \tag{2}$$

and

$$\left\{ \sum_{i=1}^{k} \alpha_i(\mathbf{n}) + \sum_{i=1}^{k} \beta_i(\mathbf{n}) + \sum_{i,j=1}^{k} \gamma_{ij}(\mathbf{n}) \right\} p(\mathbf{n})$$

$$= \sum_{i=1}^{k} \alpha_i(\mathbf{n} - \mathbf{e}_i)\, p(\mathbf{n} - \mathbf{e}_i) + \sum_{i=1}^{k} \beta_i(\mathbf{n} + \mathbf{e}_i)\, p(\mathbf{n} + \mathbf{e}_i)$$

$$+ \sum_{i,j=1}^{k} \gamma_{ij}(\mathbf{n} + \mathbf{e}_i - \mathbf{e}_j)\, p(\mathbf{n} + \mathbf{e}_i - \mathbf{e}_j), \tag{3}$$

where terms involving $p(\mathbf{m})$ with $\mathbf{m} \notin S$ are to be ignored. Where S is finite (as in any closed system), a unique stationary solution exists.

A Markov population process is reversible if it satisfies

$$p(\mathbf{n})\, q(\mathbf{n}, \mathbf{m}) = p(\mathbf{m})\, q(\mathbf{m}, \mathbf{n}) \tag{4}$$

for any pair of states $\mathbf{n}, \mathbf{m}$. Conditions equivalent to or necessary for reversibility are given by Kingman.

A process is simple if the arrival, departure, and transfer rates depend only on the numbers in the components affected by the transition, so that

$$\alpha_i(\mathbf{n}) = \alpha_i(n_i), \qquad \beta_i(\mathbf{n}) = \beta_i(n_i), \qquad \gamma_{ij}(\mathbf{n}) = \gamma_{ij}(n_i, n_j). \tag{5}$$

Kingman (1969: 7–8) showed that if $\alpha_i(\mathbf{n}) = \alpha_i(n_i)$ and $\beta_i(\mathbf{n}) = \beta_i(n_i)$ are positive functions of n_i alone, and if the process is reversible, then the stationary distribution $p(\mathbf{n})$ is given by

$$p(\mathbf{n}) = \prod_{i=1}^{k} f_i(n_i), \tag{6}$$

where

$$\frac{f_i(n_i + 1)}{f_i(n_i)} = \frac{\alpha_i(n_i)}{\beta_i(n_i + 1)}, \qquad n_i = 0, 1, \ldots, \quad \text{and} \quad \sum_{n_i=0}^{\infty} f_i(n_i) = 1. \tag{7}$$

Such a process need not be simple, since the $\gamma_{ij}(\mathbf{n})$ need not depend solely on n_i and n_j. Result (6) implies that the numbers n_i of individuals in each component are mutually independent in open systems. Hence in open systems, f_i is the marginal probability density function of n_i.

3. Stationary Distributions

Given $\alpha_i(n_i)$ and $\beta_i(n_i)$ as required by Kingman's theorem, the further requirement of reversibility (4) may easily be shown to be met by taking $\gamma_{ij}(\mathbf{n}) = 0$, in which case there are no transfers among components, or by taking

$$\gamma_{ij}(\mathbf{n}) = g_{ij}\beta_i(n_i)\,\alpha_j(n_j), \qquad g_{ij} = g_{ji}, \tag{8}$$

where g_{ij} may depend on any of the components of $\mathbf{n}$ except n_i and n_j. In this case (8), a transfer from i to j occurs at a rate proportional to the usual rate of departure from i and proportional to the usual rate of arrival to j, scaled by a factor g_{ij} which might be some measure of geographical, genetic, or psychological proximity.

For purposes of application, three special cases, two open and one closed, are of interest. In the first (Model I), arrivals and departures satisfy

$$\alpha_i(n_i) = a_i + b_i n_i, \qquad \beta_i(n_i) = d_i n_i, \qquad a_i, b_i, d_i > 0, \qquad b_i < d_i \tag{9}$$

but there are no transfers, $\gamma_{ij} = 0$. (The last inequality in (9) is necessary to obtain a stationary distribution.) In the second (Model II), arrivals and departures satisfy (9) and transfers satisfy (8) or (11). By Kingman's theorem (6) and (7) and by Katz's (1945) derivation of probability density functions from difference equations, the numbers of individuals in each component n_i are independently negative binomially distributed:

$$f_i(n_i) = \binom{r_i + n_i - 1}{n_i} p_i^{r_i} q_i^{n_i} \qquad \begin{array}{l} q_i = b_i/d_i, \qquad p_i = 1 - q_i \\ r_i = a_i/b_i, \qquad n_i = 0, 1, \dots . \end{array} \tag{10}$$

In the limit as $b_i \downarrow 0$, it may be shown from (7) (Katz 1945) or directly from (10) that the negative binomial distribution approaches a Poisson distribution. For $b_i < 0$, the distribution of n_i is binomial.

In the third case (Model III), $\alpha_i \equiv \beta_i \equiv 0$ but transfers occur, as in Model II, with rate

$$\gamma_{ij}(\mathbf{n}) = g_{ij}\, d_i n_i(a_j + b_j n_j), \quad g_{ij} = g_{ji}, \quad a_j, b_j, d_j > 0, \quad b_j < d_j, \quad i \neq j. \tag{11}$$

It follows easily from (3) that $p(\mathbf{n})$ may be written in the form (6) and $f_i(n_i)$ of Model III also satisfies the difference equation

$$f_i(n_i + 1)/f_i(n_i) = (a_i + b_i n_i)/[d_i(n_i + 1)].$$

But because of the constraint $n_1 + \cdots + n_k = n$, $f_i(n_i)$ is no longer (as it was in the open models) the marginal probability of n_i individuals in component i.

For the case $a_i = a$, $b_i = b$, $d_i = d$, Kingman (personal communication, 20 October 1971) established that

$$p(\mathbf{n}) = \prod_{i=1}^{k} \binom{-r}{n_i} \Big/ \binom{-kr}{n}, \qquad r = a/b.$$

By summing $p(\mathbf{n})$ over all $\mathbf{n}$ such that $n_1 = s$ and $n_2 + \cdots + n_k = n - s$, Kingman obtained the marginal probability density function $P(s)$ of the number s of individuals in a group:

$$P(s) = \binom{-r}{s}\binom{-(k-1)r}{n-s} \Big/ \binom{-kr}{n}. \tag{11a}$$

To investigate the limiting behavior of $P(s)$, we rewrite the right side of (11a) as

$$P(s) = \binom{r+s-1}{s}\binom{(k-1)r+n-s-1}{n-s} \Big/ \binom{kr+n-1}{n}.$$

Then from results of Feller (1957: 60, problems 18 and 19), if $kr \to \infty$ and $n \to \infty$ so that

$$\frac{n}{kr} \to \frac{1-p}{p} \tag{11b}$$

then

$$P(s) \to \binom{r+s-1}{s} p^r (1-p)^s, \qquad s = 0, 1, 2, \ldots$$

which is just the negative binomial distribution. The condition (11b) is equivalent to the reasonable condition that the mean number of individuals per group n/k approach the mean $r(1-p)/p$ of the negative binomial distribution. Thus the marginal distribution of group sizes in a large closed system (Model III) approaches the marginal distribution of group sizes in open systems where the groups have no effect on each other (Model I) or where groups exchange members at rates that depend on the numbers of members in the groups left and in the groups entered (Model II).

4. Aggregation

When a permanent labelling $i = 1, 2, \ldots, k$ of each of the components of a Markov population process is not natural or operationally feasible, an alternate description in terms of the number of components of each size is desirable. Obtaining such a description means aggregating the behavior of the individual

components into a picture of the behavior of the whole system and requires some attention in systems with nonlinear interactions such as occur in Models II and III. We assume $a_i = a$, $b_i = b$, $d_i = d$, $g_{ij} = g$.

Thinking of each component i as a group of n_i individuals, we let $G(s)$ be the number of groups each containing s individuals at some particular instant of time, and $G_s = E(G(s))$ be the expectation of $G(s)$ at equilibrium. If, as above, we take $P(s)$ as the marginal probability density function of the number s of individuals in a group, then clearly

$$G_s = \sum_{i=1}^{k} P(s) = kP(s).$$

Hence for Models I and II, G_s is k times (10), and for Model III, G_s is k times (11a).

An alternate approach that yields the same end results illuminates en route more of the aggregate dynamics, the volumes of flow into and out of groups, and hence yields intermediate results that may be useful in applications of the models. Let $\delta(x, y) = 1$ if $x = y$, $\delta(x, y) = 0$ otherwise. Then for any ν,

$$\sum_{i=1}^{k} n_i^{\nu}\delta(n_i, s) = s^{\nu}G(s).$$

In addition, for any $s > 0$,

$$\begin{aligned}
dG_s/dt = &+ \text{ expected rate of departures from groups of size } s + 1 \\
&+ \text{ expected rate of arrivals to groups of size } s - 1 \\
&- \text{ expected rate of departures from groups of size } s \\
&- \text{ expected rate of arrivals to groups of size } s.
\end{aligned} \tag{12}$$

Equation (12) accounts correctly for a transfer from a group of size s to a group of size $s - 1$, which eliminates one group of size s and creates another, leaving no net effect, as well as for a transfer from a group of size $s + 1$ to a group of size $s - 1$, which creates two groups of size s at once. For groups of size $s = 0$,

$$\begin{aligned}
dG_0/dt = &+ \text{ expected rate of departures from groups of size } 1 \\
&- \text{ expected rate of arrivals to groups of size } 0.
\end{aligned} \tag{13}$$

At equilibrium $dG_s/dt = 0$ for all s. Thus from (13), the second and third terms on the right side of (12) cancel for $s = 1$; this in turn makes the second and third terms of (12) cancel for $s = 2$; and the general condition at equilibrium which results is that

$$\begin{aligned}
E \text{ (rate of departures from groups of size } s + 1) \\
= E \text{ (rate of arrivals to groups of size } s).
\end{aligned} \tag{14}$$

We now write down explicitly the expected rates of arrivals and departures for Models I, II, and III.

Model I

From (9),

$$E \text{ (rate of arrivals to groups of size } s)$$

$$= E \left(\sum_{i=1}^{k} (a + bn_i) \, \delta(n_i, s) \right) = E(G(s)(a + bs))$$

$$= G_s(a + bs).$$

$$E \text{ (rate of departures from groups of size } s)$$

$$= E \left(\sum_{i=1}^{k} dn_i \delta(n_i, s) \right) = E(G(s) \, ds) = G_s ds.$$

From (14), at equilibrium

$$\frac{G_{s+1}}{G_s} = \frac{a + bs}{d(s + 1)} \tag{15}$$

which, as has already been seen (Section 3, combining (9) with (7)), is just the difference equation defining the negative binomial distribution. Here the G_s sum to k. No other result would have been credible, since Model I is simply k independent, noninteracting replicates of a linear birth, death, and immigration process with a negative binomial stationary distribution.

Because of this independence it is easy to see that $\text{var}(G(s)) = kp(s)(1 - p(s))$ where $p(s)$ is given by (10). For $s \neq s'$, $\text{cov}(G(s), G(s')) = -kp(s) \, p(s')$.

Model II

From (11), using the independence of the n_i, and letting $n^* = E(n_i)$,

$$E \text{ (rate of arrivals to groups of size } i)$$

$$= E \left(\sum_{i=1}^{k} \left[a + bn_i + \sum_{j \neq i} g d n_j (a + bn_i) \right] \delta(n_i, s) \right)$$

$$= (a + bs) \, G_s + E \left(\sum_{j \neq i} g d n_j \right) (a + bs) \, G_s$$

$$= (a + bs) \, G_s (1 + gd(k - 1) \, n^*).$$

$$E \text{ (rate of departures from groups of size } s)$$

$$= E \left(\sum_{i=1}^{k} \left[dn_i + \sum_{j \neq i} g d n_i (a + bn_j) \right] \delta(n_i, s) \right)$$

$$= ds G_s + ds G_s g(a + bn^*)(k - 1)$$

$$= ds G_s (1 + g(a + bn^*)(k - 1)).$$

From (14),

$$(a + bs)\, G_s(1 + gd(k - 1)\, n^*) = d(s + 1)\, G_{s+1}(1 + g(a + bn^*)(k - 1)),$$

and since $n^* = a/(d - b)$,

$$\frac{G_{s+1}}{G_s} = \left[\frac{1 + gdn^*(k - 1)}{1 + g(a + bn^*)(k - 1)}\right] \frac{a + bs}{d(s + 1)} = \frac{a + bs}{d(s + 1)}\,.$$

Thus the aggregated distribution is again negative binomial. It must be so because, in spite of the nonlinear migration rates between components, the component sizes have independent and identical negative binomial distributions. As $g \downarrow 0$, Model II approaches Model I. As a, b, and d vanish but g increases in such a way that $A = gad$ and $B = gbd$ remain constant, Model II approaches Model III. In this limit, G_s behaves discontinuously, as we shall now see.

Model III

From (11),

E (rate of arrivals to groups of size s)

$$= E\left(\sum_{j=1}^{k} \sum_{i \neq j}^{k} gdn_i(a + bn_j)\, \delta(n_j, s)\right)$$

$$= E\left(\sum_{j=1}^{k} gd(n - n_j)(a + bn_j)\, \delta(n_j, s)\right)$$

$$= G_s gd(a + bs)(n - s)$$

$$= G_s(An + s(Bn - A) - Bs^2), \qquad A = gad, \qquad B = gbd,$$

$$= G_s(A(n - s) + Bs(n - s)).$$

E (rate of departures from groups of size s)

$$= E\left(\sum_{i=1}^{k} \sum_{j \neq i} gdn_i(a + bn_j)\, \delta(n_i, s)\right)$$

$$= sG_s((k - 1)A + (n - s)B).$$

Then from (14), at equilibrium

$$\frac{G_{s+1}}{G_s} = \frac{(s + r)(n - s)}{(s + 1)[(k - 1)r + n - s - 1]}\,, \qquad (16)$$

where, as in (10), $r = a/b$. In Model III, the lack of independence among groups gives a nonlinear aggregated difference equation (16) for the expected

numbers of groups of each size. Kingman (personal communication, 20 October 1971) observed that the marginal probability density function $P(s)$ given in (11a) also satisfies this difference equation, as it must.

White's General Attractor Model

The methods just used give with equal facility the aggregate equilibrium equations of Markov population processes whose defining rates are considerably more complex. For example, the rates defining White's (1962: 156–159) general attractor model are:

$$\alpha_i(\mathbf{n}) = \alpha G(1)(1 - \delta(n_i, 0)),$$
$$\beta_i(\mathbf{n}) = \mu n_i(1 - \delta(n_i, 1)), \tag{18}$$
$$\gamma_{ij}(\mathbf{n}) = 0.$$

It is easily seen that since no arrivals can occur to groups of size zero and no departures can occur from groups of size one, the number $k - G(0)$ of groups with one or more individuals in them (the only observable groups in some circumstances) is constant. Then as in previous calculations

Rate of arrivals to groups of size s $(s > 0)$
$$= \alpha G(1)\, G(s),$$

Rate of departures from groups of size s $(s > 0)$
$$= \mu s G(s)(1 - \delta(s, 1)).$$

From (14) one obtains the same difference equations for the aggregated variables that Goodman (1964: 173–175) obtained in discussing this model.

A virtue of presenting this model in terms of the elementary rates (18) instead of in terms of aggregated variables, as White (1962) did originally, is that a candidate for the stationary distribution of the process can be tested directly through (3). Since White (1962) proposed the general attractor model as a process in which groups have truncated Poisson stationary distributions, we substitute the trial solution

$$p(\mathbf{n}) = \prod_{i=1}^{k} \frac{\lambda_i^{n_i}}{n_i!(e^{\lambda_i} - 1)}$$

and the rates (18) into (3). By symmetry of (18), $\lambda = \lambda_i$, so that (3) simplifies to

$$\alpha G(1)[k - G(0)] + \mu[n - G(1)] = \frac{\alpha G(1)}{\lambda}[n - G(1)] + \mu \lambda[k - G(0)]$$

which would be satisfied exactly if

$$\lambda = \frac{n - G(1)}{k - G(0)}$$

were a constant. The denominator is already known to be a constant. The lower the variance over time of λ at equilibrium, the more closely the stationary distribution of each group's size approaches a truncated Poisson distribution, as Goodman (1964) also pointed out.

5. APPLICATION I: SYSTEMS OF SOCIAL GROUPS

Systems of freely forming social groups arise when a large number of individuals gather but no particular associations among them appear to be externally imposed. If the individuals are nonhuman primates, the larger aggregation, usually a breeding unit, may be called a troop. A smaller, more temporary face-to-face social clustering (such as a grooming pair or a play group) within a troop may be called a group. A more precise operational definition of such freely forming groups appears in Cohen (1971). In this section, each component of a Markov population process is identified with such a group in order to study associations within a troop. In Section 6, each component of a Markov population process is identified with a whole troop (breeding unit) in order to study the dynamics and interactions of whole demes within a species.

If the individuals in a social setting are humans, the larger aggregation of interest is what Goffman (1963: 24) calls an unfocussed gathering, and the smaller aggregation, here identified with a component of a Markov population process, has been called variously a "casual" or "spontaneous" or "freely forming" group.

In applying Models I, II, and III to systems of social groups, the parameter a_i can be thought of as the attractiveness to an outsider of belonging to group i, b_i as the average attractiveness to an outsider of an individual in group i, d_i as the average propensity to depart from group i of an individual in group i; and given these characteristics of individual groups, g_{ij} may be thought of as a proximity between group i and group j.

Because of the nonlinearities in the transfer rates γ_{ij}, if there are no individuals in groups other than those of size s then there are no arrivals to groups of size s from other groups within the system. This reasonable characteristic of these Markov population processes makes them a substantial improvement over the linear one-step transition (LOST) models for systems of social groups (Cohen 1971: Chap. 4). In those models, because terms describing arrivals to groups of a given size are independent of the numbers of isolates in the system, an isolate in the system must have a propensity to join a group which is actually inversely proportional to the number of isolates in the system. Thus, according to the LOST models if the number of isolates in a system were doubled but the number of groups of size three were held constant, then an isolate's inclination to join a triple would have to be halved, in order to guarantee a constant rate

of arrival to groups of size three. Such a psychology is not impossible, but seems far less plausible than the psychology implicit in the rates of the Markov population process models.

Detailed identification of a Markov population process with social data requires some permanent labelling of groups. None of the available data on human social groups identify the groups by geographical position or by the individuals in them, so the finest details cannot be tested with such data.

But the predictions of Model II regarding aggregate rates of arrival to and departure from groups of each size have in fact already been tested and confirmed, although with another model in mind. The dynamics of an open LOST model were tested against observations of human children at play (Cohen 1971, Chap. 5) by plotting aggregate rates of arrival and departure as functions of group size, estimating from fitted straight lines parameter values corresponding to a, b, and d, and showing that these values were consistent with the estimates of a/d and b/d obtained by fitting a truncated negative binomial distribution satisfying (15) to the marginal distribution of group sizes. Fortunately, in spite of γ_{ij} being nonlinear, the aggregate arrival and departure rates of Model II in Section 4 are also linear functions of group size, and the ratios corresponding to a/d and b/d in these functions ought also to be consistent with the negative binomial marginal distribution of group sizes. Hence the nursery school data support equally Model II's dynamics for an open system of casual social groups.

The aggregate or marginal distribution (16) of the number of groups of each size predicted by Model III can now be tested with Struhsaker's (1965) observations of a (nearly) closed vervet monkey troop.

Table 1 presents Struhsaker's observed frequency distribution of vervet sleeping group sizes (including nights when some animals in the troop were not seen), the expected numbers G_s of groups of each size s according to the difference Eq. (16) predicted by Model III, and a previously fitted (Cohen 1971: 18) truncated negative binomial distribution, predicted by a closed LOST model.

To estimate r, a computer routine accepted fixed values for k and n, calculated G_s iteratively by (16), normalized G_s so that they summed to the total number of groups observed, and searched for that value of r which minimized Pearson's X^2. The same pooling of frequency classes for fitting G_s was followed as had been previously adopted for fitting the truncated negative binomial. The routine was verified by finding that it recovered the value of r which had been used to generate by hand a set of artificial data which exactly matched the expected values G_s.

The number of monkeys in the troop was $n = 17$, and the maximum number of separate sleeping groups observed on any night when all animals in the troop were accounted for was $k = 6$ (Cohen 1971: 15). (Conveniently, the minimum

TABLE 1

Marginal Frequencies (Column 2) of Group Sizes (Column 1) Observed by Struhsaker in a Closed Vervet Monkey Troop; Expected Frequencies According to Model III (Column 3) and a Truncated Negative Binomial Distribution (Column 4); and Expected Frequencies According to Model III (Column 5) Fitted to the Negative Binomial Distribution (Column 4)

(1) Group size s	(2) Struhsaker's observed frequency	(3) Model III G_s	(4) Truncated negative binomial	(5) G_s fitted to truncated negative binomial
1	27	35.5	28.3	35.5
2	29	25.6	26.8	25.8
3	24	19.6	22.8	19.9
4	20	15.4	18.2	15.6
5	12	12.2	14.0	12.4
6	9	9.7	10.5	9.8
7	5	7.7	7.7	7.7
8	4	6.0	5.6	6.0
9	9	4.6	4.0	4.5
10	2	3.5	2.8	3.4
11	2	2.6	2.0	2.5
12	0	1.8	1.4	1.7
13	3 {1	2.0 {1.2	1.7 {1.0	1.8 {1.1
14	{2	{0.8	{0.7	{0.7
15	{0	{0.4	{0.5	{0.4
16	1 {0	0.7 {0.2	1.4 {0.3	0.6 {0.2
⩾ 17	{1	{0.1	{0.6	{0.1
	$k = 6$ $n = 17$	$r = 0.64$ $X^2 = 13.803$ $df = 12$ $0.3 < P < 0.5$	$r = 1.92$ $p = 0.35$ $X^2 = 11.599$ $df = 11$ $0.3 < P < 0.5$	$r = 0.67$ $X^2 = 3.996$

values of X^2 corresponding to the alternate parameter values $k = 5$ and $k = 7$ are higher than the X^2 with $k = 6$.) To the nearest 0.005, the value of r which minimizes X^2 when $k = 6$ and $n = 17$ is 0.640. While the corresponding value of $X^2 = 13.803$ is higher than the $X^2 = 11.599$ obtained for the fit to the truncated negative binomial distribution, the negative binomial has one more free parameter. Since the probability levels P associated with the values of X^2 in both cases satisfy $0.3 < P < 0.5$, the difference in fit between the negative binomial and G_s is negligible.

To illustrate how closely the distribution G_s can approximate a negative binomial distribution with parameter values as far from infinity as $k = 6$ and $n = 17$, the last column of Table 1 shows the result of fitting G_s to the expected

values of the negative binomial distribution which had been previously fitted to the data. Taken strictly as a numerical index without probabilistic interpretation, $X^2 = 3.996$ suggests a close fit.

The negligible difference in goodness of fit to aggregated data between the closed LOST model, which assumes linear arrivals to groups, and Model III which assumes nonlinear transition rates, suggests once again the inadequacy of aggregated data alone to discriminate among alternate possible detailed mechanisms. A more important difference between the two models than goodness of fit is the difference between the estimated values of r, the ratio of group attraction to individual attraction. Fitting the negative binomial gives an estimated $r = a/b$ of 1.9. The value of $r = 0.6$ obtained here by fitting G_s accords more closely with the still very tentative speculation (Cohen 1972) that there may be a phylogenetic trend within the primates toward a rising value of r: an ascendancy of group attraction over individual attraction in systems of casual social groups. Perhaps the most important difference between the two models, and one which seems decisively to favor Model III, is the superiority of the behavioral assumptions of Model III.

While a Markov population process offers the possibility of a much finer analysis than do the LOST models of the aggregated consequences of variability in the characteristics of groups and their interconnections, many analytical questions remain unsolved. For example, what is the stationary distribution $p(\mathbf{n})$ when $g_{ij} \neq g_{ji}$?

At an even finer level than Markov population processes, one hopes for models which specify the characteristics of mobility of individuals, and for which sufficient analytical machinery is available to permit aggregation first to groups and thence to the system as a whole. See White (1970).

6. APPLICATION II: POPULATIONS OF BREEDING UNITS (TROOPS)

Each component of Model I is a linear birth and death process with immigration, or a birth-immigration–death-emigration (BIDE) model. The stationary distribution of each component, the negative binomial distribution, fits with fair accuracy the observed aggregated size distributions of troops (breeding units) of a number of primates, including howler monkeys, gibbons, colobus, langurs, and baboons (Cohen 1969). The very few data available on the size distribution over time of a single primate troop (Altmann and Altmann 1970: 31) were insufficient for testing whether that troop's size distribution was negative binomial; hence aggregated numbers of troops of each size, corresponding to G_s, were analyzed on the basis of the explicit assumption (Cohen 1969: 473) that immigrations to each troop were independent of emigrations from all other troops.

Some evidence contradicts this assumption. Altmann and Altmann (1970: 47–57) observed in detail several transfers among baboon troops by adult males. They review (1970: 63–64) other cases of migration between troops described elsewhere. Schaller (1965: 337–338) observed several migrations of adult gorillas, both male and female, between what he called groups and what are here called troops. Yoshiba (1968: 235–237) reported changes in the lead male of six langur troops as a result of contacts between those bisexual troops and all-male troops. A Japanese macaque, instead of entering another troop, recruited a troop around himself from the membership of a larger troop (Frisch 1968: 247).

This list of well-attested cases of migration between troops, which makes no pretensions of completeness, excludes many inconclusive observations of what may be migrations between troops (e.g., Carpenter 1965: 269–270; Reynolds and Reynolds 1965: 396). Altogether, the available observations are too few or too imprecisely reported to make possible credible estimates of rates of intertroop migration, although in the best case (baboons) some lower bounds might be guessed.

D. S. Sade (personal communication, July 1970) has objected to the BIDE model's assumption that the rates of immigration to a troop are independent of its size, and has suggested that the rate of immigration increases with troop size. If this is so, transfer rates which ignore the size of the receiving troop must at a minimum be replaced by transfer rates of the form (11), and two parameters, not one, must be estimated from observations: the rate $g_{ij} d_i a_j$ (per monkey in the troop left per day) of transfers which do not depend on the receiving troop's size, and the rate $g_{ij} d_i b_j$ (per monkey in the troop left per monkey in the troop entered per day) of transfers which depend on the numbers of monkeys in both troops. Clearly estimation of these rates requires knowledge of the sizes of both the troop left and the troop entered. A field worker who invites home a realistic model has opened the door to a creature with an enormous appetite for costly quantitative data. Yet if quantitative studies of the genetic structure of primate populations are to have a firm foundation in population dynamics, there is no other choice.

7. Additional Markov Population Processes and Generalizations

Kingman (1969) reviewed a variety of probabilistic models which could be formulated and analyzed as Markov population processes. Three more examples, and two generalizations, all unavailable when he wrote, complement his list.

Puri (1968) studied by ad hoc methods linearly interconnected birth and death processes which are simple in the sense of (3).

His defining rates were:

$$\alpha_i = \lambda_i n_i \,,$$
$$\beta_i = \mu_i n_i \,,$$
$$\gamma_{i,i+1} = \nu_i n_i \,, \qquad \lambda_i \,, \mu_i \,, \nu_i \,, \delta_i > 0,$$
$$\gamma_{i,i-1} = \delta_i n_i \,,$$
$$\gamma_{ij} = 0 \qquad \text{if} \quad j \neq i \pm 1.$$

Matis and Hartley (1971) allowed arbitrary linear connections from one component to another, but no immigration. Their parameters were:

$$\alpha_i = 0,$$
$$\beta_i = b_{oi} n_i \,,$$
$$\gamma_{ji} = b_{ji} n_i \,.$$

Milch (1968), by Herculean calculations, derived the transition probabilities from the rates of a process which has no transfers between components, but which is not simple. His defining rates were:

$$\alpha_i = (n + 1) p_i \,,$$
$$\beta_i = n_i \,,$$
$$\gamma_{ij} = 0.$$

Port (1968a) studied a model which is identical to a Markov population process except that more than one individual can arrive at a component simultaneously. Port (1968b) generalized the arriving stream of clusters of individuals from a Poisson process to an arbitrary renewal process.

Additional examples of multidimensional stochastic processes are reviewed by Whittle (1964).

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