GROUPING IN A VERVET MONKEY TROOP

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The question of who sleeps with whom interests primates of several species, and for varied reasons. A wild East African vervet monkey has a participant's lively interest in the formation of sleeping groups every evening within his troop. To a human observer of a vervet troop, the formation of sleeping groups offers an opportunity to improve understanding of social behavior and organization in an evolutionary perspective. It offers an opportunity also to try to link, through the mediation of its society, the individual behavior and population ecology of a species.

Previous studies of freely-forming small groups of humans showed that the observed frequency distributions of group size were usually very closely described by the Poisson distribution with the zero value truncated [COLEMAN and JAMES, 1961]. Several models, based on widely varying assumptions, were proposed to account for the observed regularity [COLEMAN, 1964; WHITE, 1962; GOODMAN, 1964]. The multiplicity of these models posed the challenge of finding data that would discriminate among them. Nonhuman primate data with the necessary degree of detail offered the further possible advantage of conforming only to a model of some evolutionary generality.

During a year's field study of wild vervet monkeys *(Cercopithecus aethiops)* in East Africa, STRUHSAKER recorded individual by individual the composition of the sleeping groups of a particular troop on 22 nights. On an additional 16 nights he was able to observe the composition or size of some, but not all, of the sleeping groups of the troop [STRUHSAKER, 1965, 1967, and personal communication]. The frequency distribution of the sizes of these groups cannot be described by a truncated Poisson distribution, so the models constructed for human groups cannot apply directly to the monkeys.

However, the frequency distribution of the sizes of the monkey groups is well described by a negative binomial distribution with the zero value truncated (table I). A truncated negative binomial distribution can arise as a compound truncated Poisson distribution. Finer analysis of the data shows, however, that the distribution of group sizes is not a time-varying truncated

Table I. Frequency distribution of size of sleeping groups in a troop of vervet monkeys
(Cercopithecus aethiops)

(1)		(2)	(3)		(4)		(5)
Group size		Observed	Predicted		Observed		Predicted
1		19	18.9		27		28.3
2		14	17.1		29		26.8
3		19	14.1		24		22.8
4		11	11.0		20		18.2
5		7	8.3		12		14.0
6		7	6.2		9		10.5
7		3	4.5		5		7.7
8		2	3.2		4		5.6
9		3	2.3		9		4.0
10		1	1.6		2		2.8
11		2	1.1		2		2.0
12	1 {	0	1.4 {	0.8	0		1.4
13		1		0.6	1	1.7 {	1.0
14	2 {	2	1.2 {	0.4	3 {		0.7
					2		
15		–		–	0	1.4 {	0.5
16		–		–	1 { 0		0.3
17		–		–	1		0.2

(1) Number of animals in group.
(2) Observed frequency according to STRUHSAKER [1965, table 51] on nights when all animals in the troop were seen.
(3) Predicted frequency according to a fitted truncated negative binomial distribution. $X^2 = 5.23$ with 10 degrees of freedom; $0.8 < p < 0.9$.
(4) Observed frequency according to (2) plus THOMAS T. STRUHSAKER [personal communication, 17 June 1968], including nights when some animals in the troop were not seen.
(5) Predicted frequency according to a fitted truncated negative binomial distribution. $X^2 = 11.60$ with 11 degrees of freedom; $0.3 < p < 0.5$. Data published by kind permission of Dr. STRUHSAKER.

Poisson; nor is it compounded of truncated Poisson processes associated with each individual, the parameters of which vary from one monkey to another. Thus plausible attempts to reduce the formation of groups to a mixture of human-like truncated Poisson processes fail.

A combinatorial model [ALTMANN, 1965] which counts the number of arrangements of distinguishable individuals into indistinguishable groups and assumes all such arrangements equiprobable fails to approximate the observed distribution of number of groups per night. Another combinatorial model succeeds in approximating both the distribution of number of groups per night and the distribution of group sizes with the help of an *ad hoc* assumption that no more groups may exist than were observed on the night with the highest number of groups. This model counts the number of arrangements of indistinguishable individuals in indistinguishable groups. But the model must be rejected because it assumes the monkeys to be indistinguishable, and because it predicts only monotonic decreasing frequency density functions.

A family of simple stochastic models, formally like some of the models previously proposed for the human data, involves rates of joining and leaving groups which are linear functions of group size. The number of isolates or groups of size one in the system is assumed to affect directly only the formation of pairs, and then to have no direct effect on the formation of larger groups.

To be interpretable, these models, called the linear one-step transition (LOST) models, can have only two independent parameters. The models assume that individuals join groups because of the attraction either of group membership or of individuals in the group, and leave groups because of individuals in the group. The first parameter describes the ratio of the rate of joining because of group membership to the rate of leaving, while the second parameter describes the ratio of the rate of joining because of individuals in groups to the rate of leaving. In the interpretable ranges of these parameters, the models predict at equilibrium a distribution of group sizes given by the truncated negative binomial distribution. A special value of one of the parameters leads to the truncated Poisson distribution.

The behavior of isolates can be so specified that the models describe either a closed system of groups with a fixed number of individuals or an open system with a variable number of individuals in which the number of groups is constant. In either case the equilibrium distribution remains the same.

Numerical solution of the system of ordinary differential equations, deterministically interpreted, which define the open and closed models gives information about how average systems of groups move toward equilibrium from various initial conditions. When the rate constants of these models are

actually estimated from the flux of individuals among groups instead of from the presumed equilibrium distribution, as at present, this information about rapidity of approach to equilibrium will make possible a decision as to whether a particular system of groups is near equilibrium.

The detailed mechanisms of group formation assumed by these open and closed LOST models of group formation are so simple that they should be easily tested with appropriate future data on the kinetics (the flux) of groups.

These linear stochastic models account not only for STRUHSAKER's monkey data. They account for two of the three distributions of the sizes of pedestrian human groups which had previously resisted interpretation [COLEMAN, 1964]. They account for at least two of the possibly biased distributions of the sizes of sleeping groups of four other species of monkeys observed in Uganda [LUMSDEN, 1951]. And they account for the distribution of occupancy of passenger cars on the freeways of Los Angeles [HAIGHT, 1960].

In at least two instances, the LOST models also fail to predict observed distributions when the assumptions underlying the predictions are clearly violated. Thus the LOST models offer some possibility of understanding why good predictions are obtained when they are obtained.

STRUHSAKER's social data reveal interesting individual differences among the monkeys. Whereas the relative frequency of isolates among groups is, as expected, binomially distributed when the identity of the monkeys is ignored, the relative frequency of isolation for each monkey departs strikingly from the expected binomial distribution. Obvious factors such as age, sex, and social rank do not in most cases explain why some monkeys slept alone much more often than expected and others never.

The formation of sleeping groups seems to be one area of the troop's social life where dominance is not important. The diverse social composition of these groups may impede one role proposed for the sleeping groups by STRUHSAKER: the gradual formation of new, independent troops.

Given the form of the distribution of group sizes, the parameters of the distribution can be fairly well calculated, at least in the case of human groups, from an acoustical theory which links individual requirements and capacities for understanding speech with ecological information about background noise levels. This derivation exemplifies how explicit theory can unify independent measurements of individual organisms, social organization, and the environment.

Explicit models of social organization backed by sufficient data can contribute to clearer language and more useful concepts for comparative and evolutionary discussions of human and nonhuman societies.

SUMMARY

Data collected by T. T. STRUHSAKER on sub-grouping of a wild East African *Cercopi-thecus aethiops* troop are analyzed in order to test models of group formation. The data fail to support several earlier proposed models. A new model of the formation of groups leads directly to the negative binomial distribution, includes the Poisson as a special case, and accounts for some discrepant human data. The detailed mechanisms of this proposed model should be easily testable with appropriate future information on group formation and structure.

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