

THE SIZE AND DEMOGRAPHIC COMPOSITION OF SOCIAL GROUPS OF WILD ORANG-UTANS

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Abstract. Mackinnon (1974) observed social sub-groups of wild orang-utans. The groups' distribution of size and age-sex composition can test mathematical models of group formation. As predicted by models published previously, a truncated Poisson distribution describes the group sizes well. The inferred parameters governing group formation conform to a pattern in other primate species. A simple model for the demographic composition of a sub-group assumes that an individual joins a sub-group with a probability independent of his age-sex class and of other members of the sub-group. This model's predictions, which agree poorly with observation, offer a quantitative baseline against which one can infer when a demographic combination occurs with a non-random frequency.

Many species of primates form temporary social groups within a breeding unit or population. These groups vary greatly in size and composition, over time and at any given time.

Many studies have reported the average, and sometimes the variance or range, of the numbers of individuals in such groups. The frequency distribution of group sizes has been reported for eight species of forest monkeys (Lumsden 1951), human beings (James's data in Coleman 1964; Cohen 1971a), vervets (Struhsaker 1965; data reprinted in Cohen 1971a), yellow baboons (Cohen 1971b) and orang-utans (Mackinnon 1974).

The widespread occurrence among primates of these social groups suggests that detailed quantitative study might reveal a pattern of homologies which has systematic and evolutionary significance. The seeking of evolutionary insight from comparative behavioural studies of primates is not new (Crook & Gartlan 1966). It is less common to apply to a single aspect of social behaviour the same kind of detailed quantitative comparative analysis that functional anatomists now find useful in illuminating the mechanics and evolution of the primate hand or shoulder.

Quantitative models for social groups were proposed for non-human primates by Altmann (1965) and for humans by several sociologists (Goodman 1964). Models of Cohen (1971a, 1972a) claimed utility for both human and non-human primate group size distributions. These models have been tested since their proposal

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against new observations of yellow baboons (Cohen 1971b).

My purpose here is again to test and extend these models using Mackinnon's recent observations (1974) of 'newly visiting sub-groups' of wild orang-utans (*Pongo pygmaeus*); and when the models succeed, to see if the results are consistent with a phylogenetic pattern suggested earlier (Cohen 1971a, pp. 162-163; 1972b). Where Altmann (1965) and Mackinnon (1974) used the term 'subgroup', here the term 'group' will be used for brevity. In view of the time, effort, and money required to obtain the data on orang-utans, it seems desirable to extract as much scientifically useful information from them as possible.

Methods

Tabulation and Notation

From Table X of Mackinnon (1974, p. 51) three tabulations were prepared. In each, Borneo and Sumatra data appear separately and combined. First, the frequency distribution of size of group (Table I) gives the sum of the observed frequencies of all groups with a given number of members, regardless of the composition of the groups. Second, the demographic structure of the population (Table II) is a count of the numbers of individuals observed in each age-sex class distinguished by Mackinnon (1974), regardless of the size or composition of the groups in which the individuals were observed. The five age-sex classes distinguished by Mackinnon (1974) in the numbering which is adopted for the rest of this paper, are (1) adult males (M); (2) adult females (F); (3) adolescents (A); (4) juveniles (J); and (5) infants (I). Third, the frequency distribution of the composition of

groups is simply a more systematic rearrangement by size of group and in lexicographic order (using the above ordering) of Mackinnon's Table X (Table III).

All these tabulations accept the convention of counting 'newly visiting' individuals and groups as distinct. See Mackinnon (1974) for the details and justification of this convention.

n = the size of a group; e.g. for the group FJI, $n = 3$.

g_n = the number of groups of size n , e.g. for Borneo $g_1 = 62$ means that 62 groups of size 1 (single individuals) were observed.

G = the total number of groups observed, e.g. for Sumatra $G = 45$. $G = g_1 + g_2 + \dots$

N = the total population observed in all groups; e.g. for Borneo $N = 266$. $N = 1g_1 + 2g_2 + 3g_3 + \dots$

g = the average number of individuals per group; $g = N/G$.

s_g = the standard deviation of the average number of individuals per group (equals $G^{-1/2}$ times the standard deviation of the number of individuals per group).

C = the number of age-sex classes distinguished; here $C = 5$.

N_i = the total observed number of individuals in the age-sex class i , $i = 1, 2, \dots, C$; e.g. in Borneo, $N_4 = 64$ means that 64 'newly visiting' juveniles were observed there.

n_i = the number of individuals in a group who belong to age-sex class i ; e.g. $n_1 = 2$ means a group contains two males (M).

(n_1, n_2, \dots, n_C) = a description of the demographic composition of a group; e.g. $(2, 1, 0, 0, 0)$ = MMF in Mackinnon's notation, two males and a female; $n_1 + n_2 + \dots + n_C = n$.

Π = the conventional symbol for a product.

λ = the parameter of the Poisson distribution, equal to the mean and variance when the distribution is not truncated.

p = probability that an individual will be included in a group, assumed independent and identical for all individuals.

Table I. Observed and Theoretical Frequency Distributions of Size of 'Newly Visiting' Orang-Utan Groups in Borneo and Sumatra (Observed Frequencies are Based on Mackinnon (1974). Predicted Frequencies are a Fitted Truncated Poisson Distribution with the Given Value of λ . Notation is Defined in the Text. The Values of χ^2 are not Significant at the 5 per cent Level).

Group size (n)	Borneo		Sumatra		Total	
	Observed g_n	Predicted g_n	Observed g_n	Predicted g_n	Observed g_n	Predicted g_n
1	62	69.0	23	22.1	85	91.1
2	53	46.6	11	14.2	64	60.8
3	27	20.9	9	6.1	36	27.1
4	3	7.1	2	2.0 *	5	9.0
5	1	1.9	0	0.6 †	1	2.4
6	0	0.5	0	—	0	0.7
G	146		45		191	
N	266		80		346	
g	1.822		1.778		1.812	
s_g	0.071		0.077		0.063	
λ	1.349		1.287		1.335	
χ^2	6.553		2.280		6.721	
df	3		2		3	

*Bracketed frequencies are pooled in calculating χ^2 . Independence among observed group sizes is assumed.

†Predicted frequency of groups of size five or larger.

Homogeneity

Group Size. To see whether the group size distribution in Borneo differed significantly from that in Sumatra, the difference between the average group sizes (g in Table I) in the two regions was compared to the standard deviation of the average group size (s_g in Table I) for each region. Because (as will be shown under Results) the group size distribution in each region was well described by a truncated Poisson distribution, this test based on a single sufficient statistic for each region's distribution is more powerful (more likely to detect a difference) than a homogeneity χ^2 -test based on a comparison of g_n for each value of n .

Demographic structure. The demographic structure of a population here means the distribution of individuals into age-sex classes. For each region the structure is described by the values of N_i . To test whether the distribution of N_i for Borneo differed from that for Sumatra, a simple 2×5 homogeneity χ^2 test was used.

Group Size

The models of Cohen (1971a, 1972a) predict that the distribution of group sizes will be described by a truncated Poisson distribution or a truncated negative binomial distribution. In either case, the frequencies of groups of size 0, which cannot be observed, are truncated. Since the truncated Poisson distribution is the simpler distribution, with only one fitted parameter, it was tested first.

The maximum likelihood estimate of the parameter λ of the truncated Poisson distribution was determined by finding, by trial and error, a value which satisfies the equation

$$g = \lambda / (1 - e^{-\lambda}) \quad (1)$$

As an alternative to trial and error, tables are available (Cohen 1960) which make it possible to look up λ directly, given g . The predicted number of groups of size n was calculated from

$$G \lambda^n / (n! [e^\lambda - 1]) \quad (2)$$

for each group size n actually observed. The predicted number of groups of size greater than those observed was found by subtracting from G the sum of the predictions calculated in (2).

The goodness of fit of the observed to predicted frequencies was evaluated with the χ^2 -test. The number of degrees of freedom (df) was two less than the number of observed frequencies being tested. One df is deducted because the

sum of the predictions must be G , and another because λ is estimated from the data.

Group Composition

The models for group formation of Cohen (1971a, 1972a) pay no attention to possible differences in social behaviour according to age-sex class, though they do not necessarily assume that no such differences exist.

The assumption that indeed no such differences exist, that, for example, there are no special attractions or repulsions between individuals of the same or different age-sex classes, will now be made the basis of a model of the distribution of the age-sex composition of social groups. Based on an implausibly simple assumption, this model may be viewed as a null hypothesis against which observed deviations may be assayed.

Suppose then that social groups are formed by independent Bernoulli sampling of each of the N members of the population, each member having identical probability p of inclusion in a group. More picturesquely, suppose the N individuals in the population are lined up. A group is formed by proceeding down the line and flipping a coin once for each individual. The probability that the coin comes up heads is p . If the coin comes up heads, the individual is included in the social group; otherwise, not.

The number of individuals belonging to a group generated by this procedure ranges from 0 to N , with average group size pN (including the cases when the group finally obtained is empty). For consistency with the observations of group size, this average group size pN must equal the average group size λ of the group size distribution when that distribution also includes groups of size zero. This consistency requirement gives a simple way to estimate p :

$$p = \lambda / N \quad (3)$$

Then the probability that a particular specified set of n individuals will be chosen from the population of N individuals is $p^n (1-p)^{N-n}$. The number of ways this group can contain exactly n_i individuals from age class i , which is represented by N_i individuals in the population, is just $\binom{N_i}{n_i}$ or $N_i! / (n_i! [N_i - n_i]!)$. Hence if G groups are observed, the predicted (or expected) frequency of an observed group with composition (n_1, \dots, n_c) is

$$\frac{G}{1 - (1-p)^N} p^n (1-p)^{N-n} \prod_{i=1}^c \binom{N_i}{n_i} \quad (4)$$

The factor dividing G in (4) excludes the probability of an empty group, which could not be observed; thus the group (0...0) is truncated here as in the group size distribution. (For large values of N and small values of p , it may be shown that when λ is estimated from (1) the maximum likelihood estimate of p under the model (4) is given by (3).)

To illustrate the calculation of (4), the expected frequency of the group MFAAJ for the combined populations will be calculated. In this case

$$p = \lambda/N = 1.335/346 = 3.8584 \times 10^{-3}$$

Then $G/(1 - (1 - p)^N) = 258.9759$ is the number of groups that would have to be formed by the procedure assumed in the model in order that the expected number of observable (that is, non-empty) groups be $G = 191$

$$p^5(1 - p)^{341} = 2.2883 \times 10^{-3}$$

is the probability that a group will contain any specified set of five particular individuals from the population of $N = 346$ individuals; and the number of ways of drawing five individuals to get the group composition (1, 1, 2, 1, 0) is $83 \times 111 \times (30 \times 29/2) \times 73 \times 1$. The product (4) is 0.017; which is rounded in Table III to 0.0+.

No formal test of the goodness of fit of predictions to observations was performed, for reasons that will be apparent (Table III).

Calculations

All calculations were done on a Hewlett-Packard hand calculator, model HP-35. No computer was necessary. All intermediate results

were recorded to at least four significant figures and rounded only in the final tabulations. Some rounded totals may not coincide with the sum of rounded summands.

Results

Homogeneity

The mean observed group size in Borneo differed from the corresponding mean in Sumatra by less than the smaller of the standard deviations of the two means (Table I). No significant difference in means could be inferred. Because the means characterize the truncated Poisson distribution (see below), the distributions of group size in the two regions did not differ significantly.

The χ^2 -test for a difference in age-sex structure between the two regions was not significant at the 5 per cent level (Table II). This result endorses post facto Mackinnon's (1974) pooling of his observations from both regions to estimate orang-utan population structure.

Group Size

The predicted frequencies of groups of each size accompany the observations in Table I. The χ^2 -test of goodness of fit reveals no difference between predicted and observed frequencies significant at the 5 per cent level, for Borneo or Sumatra separately or combined. Additional tests not described here on the combined data (a truncated Poisson variance test and Sampford's criteria for existence of a solution to the moment-matching equations of the truncated negative binomial distribution;

Table II. Observed and Theoretical Frequencies of Age-Sex Classes in 'Newly Visiting' Orang-Utan Groups in Borneo and Sumatra (Observed Frequencies are Based on Mackinnon (1974). Predicted Frequencies Assume Homogeneity of the Demographic Structures of the Borneo and Sumatra Populations. The Value of χ^2 is Not Significant at the 5 per cent level.)

Age-sex class (<i>i</i>)	Borneo		Sumatra		Total Observed N_i
	Observed N_i	Predicted N_i	Observed N_i	Predicted N_i	
1. Male (M)	58	63.8	25	19.2	83
2. Female (F)	85	85.3	26	25.7	111
3. Adolescent (A)	22	23.1	8	6.9	30
4. Juvenile (J)	64	56.1	9	16.9	73
5. Infant (I)	37	37.7	12	11.3	49
Total (N)	266		80		346

$\chi^2 = 7.402$, $df = 4$. Independence among observations of age-sex class is assumed.

details and references in Cohen 1971a) confirm the appropriateness of the truncated Poisson distribution and the inappropriateness of the truncated negative binomial distribution.

The finding that each distribution separately is approximately truncated Poisson justifies the use of the mean for a test of homogeneity above. The finding that the combined populations also fit a truncated Poisson further confirms the homogeneity of the two group size distributions. Visual inspection of Table I reveals good agreement with the truncated Poisson

distribution, with the slight suggestion of a possible deficit of observed groups of size four and larger. Inferences about the dynamics of social behaviour will be offered in the Discussion.

Group Composition

The predicted frequencies of groups having each of the compositions observed appear in Table III. The predicted frequencies for the combined populations of Borneo and Sumatra do not equal exactly the sum of the frequencies

Table III. Observed and Theoretical Frequency Distributions of Age-Sex Composition of 'Newly Visiting' Orang-Utan Groups in Borneo and Sumatra (Observed Frequencies are from Mackinnon (1974). Predicted Frequencies are from Equation (4).)

Group composition	Borneo		Sumatra		Total	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
M	40	15.1	13	6.9	53	21.9
F	4	22.1	5	7.2	9	29.2
A	10	5.7	5	2.2	15	7.9
J	8	16.6	—	—*	8	19.2
MF	1	6.5	2	2.9	3	9.4
MA	—	—	1	0.9	1	2.5
MJ	1	4.9	—	—	1	6.2
FA	1	2.5	2	0.9	3	3.4
FJ	32	7.2	5	1.1	37	8.3
FI	16	4.2	1	1.4	17	5.5
AA	1	0.3	—	—	1	0.4
AJ	1	1.9	—	—	1	2.2
MMF	1	0.9	—	—	1	1.5
MFJ	5	2.1	—	—	5	2.7
MFI	4	1.2	7	0.6	11	1.8
MAA	1	0.1	—	—	1	0.1
FFJ	1	1.5	—	—	1	1.8
FAJ	1	0.8	—	—	1	1.0
FAI	1	0.5	—	—	1	0.6
FJI	13	1.4	2	0.2	15	1.6
MFAI	2	0.1	—	—	2	0.2
MFJI	1	0.4	2	0.1	3	0.5
MFAAJ	1	0.0+	—	—	1	0.0+
Other not observed	—	50.0	—	20.6	—	50.2

*The predicted frequencies of groups not observed are pooled under 'Other not observed'.

predicted for each population separately. The reason is that the separate predictions for Borneo and Sumatra are based on estimates of p and N_i appropriate to the separate populations, while the predictions for the combined populations are based on estimates of p and N_i for the combined populations.

Even without a formal statistical test, inspection of Table III shows that the agreement between prediction and observation is poor. If the homogeneity of the populations with respect to group composition is accepted, a comparison for the combined populations suffices. This comparison shows that markedly more groups of the following composition were seen than predicted: M, A, FJ, FI, MFI, FJI. Among the group compositions that were observed at all, these were observed markedly less frequently than predicted: F, J, MF, MJ. In addition a great many more groups with a predicted total frequency of 50.2 for the combined population were not observed at all. (It is of course inevitable that most of the many possible demographic combinations not appear at all in a sample of only 191 groups.)

The clear conclusion is that membership in a social group cannot be assumed to have a probability that is independent and identical for every orang-utan, regardless of age-sex class.

Discussion

Homogeneity

In spite of the considerable geographical separation between the orang-utan populations of Borneo and Sumatra and the difference in their habitats noted by Mackinnon (1974), there is no significant evidence of differences between them in either the distribution of group sizes or in their demographic structure. On this basis the combined orang-utan population (for at least these two regions) may be discussed as a whole.

Group Size

Mackinnon's observations (1974) are the first sufficiently numerous, detailed, and quantitative to make possible a test on a great ape of mathematical models for the formation of social groups among primates. The test neatly confirms the equilibrium predictions of the models. The observed group size distributions are well described by truncated Poisson distributions. The dynamic assumptions of the models, that is, the assumed processes of change in social group

membership, cannot be tested directly with these data.

The model which seems most appropriate to Mackinnon's description of orang-utan social groups is model II of Cohen (1972a). This 'open' model allows entry to the system of social groups by birth or immigration and exit from the system by death or emigration. It also includes migration of individuals from one social group to another.

In this model, a parameter a describes the probability, per unit time per individual outside of a given group, of attraction to a given group, regardless of the size of the group. This parameter summarizes the attractiveness of groups per se. A parameter b describes the attractiveness (that is, the probability of joining, per unit time per individual outside a group) of a group per individual in the group. The overall attractiveness of a group is the attractiveness of group membership per se plus the attraction of the n individuals in the group: $a + bn$. Finally, a parameter d describes the probability of departure from a group, per unit time per individual in the group. Thus the probability per unit time of a departure from a group of size n is dn .

The parameters a , b , and d of model II are related to the parameter of a truncated Poisson distribution by $\lambda = a/d$. Because the truncated Poisson describes the data, the additional parameter of the negative binomial distribution need not be used. Therefore $b/d = 0$.

That $a/d = 1.335$ while $b/d = 0$ means that the attraction of group membership per se is more important than the average attractiveness of an individual already in a group. Since 'group' here includes groups of size one, or single individuals, this interpretation also means that the satisfactions of isolation exceed the average attractiveness of other individuals in groups.

This result is consistent with a previously noticed pattern (Cohen 1971a, pp. 162 to 163; 1972b) in the estimates of the parameters a/d and b/d (Table IV): the magnitude (or importance) of individual attraction relative to group attraction (b/d relative to a/d) declines as the phylogenetic distance of non-human primates from man declines. Orang-utans provide further evidence that the quantitative parameters of models of social behaviour can provide a coherent comparative schematization of one aspect of social behaviour. This schematic description offers a useful alternative to typological descriptions of social behaviours.

Table IV. Median Values of the Parameters a/d and b/d for Some Living Primates. (All Values Except Those for Orang-Utans are from Cohen (1972b, p. 425). Parameter a Measures Group Attractiveness, b Individual Attractiveness, d Individual Departure Rate.)

Primate (Human observer)	a/d	b/d
Vervets, <i>Cercopithecus aethiops</i> (Struhsaker)	1.15	0.66
Yellow baboons, <i>Papio cynocephalus</i> (Cohen)	0.12	0.16
Human 4-year-olds, <i>Homo sapiens</i> (Cohen)	0.33	0.10
Mixed humans, <i>Homo sapiens</i> (James)	0.86	0
Orang-utans, <i>Pongo pygmaeus</i> (Mackinnon)	1.34	0

Group Composition

The comparison of observed and predicted frequencies of group composition in Table III justifies an unsurprising conclusion. Demographic characteristics (age and sex) influence the composition of social groups of orang-utans.

Males and adolescents appeared by themselves much more often than expected. Females and juveniles appeared alone much more rarely than expected. The group consisting of a single infant I, with a predicted frequency of 12.9, did not appear at all.

With five age-sex classes, there are fifteen possible compositions of a group of size two. On the basis of (4), the six couples predicted to be most frequently observed are MM, FF, MF, MJ, FJ, FI (though not in this order). Of these six, the first four were observed markedly more rarely than expected (indeed, MM and FF were not observed at all), and the last two much more often than expected.

A finding that might not have been anticipated and could not be confirmed without a quantitative 'random' model to set a baseline, is that MF couples, without accompanying young, were notably rarer than expected, while MFI triples were more frequent.

The model which leads to equation (4) assumes that the probability p of group membership is the same for all age-sex classes. A slightly more sophisticated model would assume instead that each class has its particular probability p_i , $i = 1, \dots, C$, but would retain the other assumption of independence between individuals. Tests of this model, not described here, reveal that it too describes the data inadequately. This failure suggests that a successful model of group composition will have to incorporate a representation of the interactions within and between age-sex classes.

No model now available can predict quantitatively the demographic details of group composition in Mackinnon's (1974) orang-utan data, or the even more detailed data due to Struhsaker (1965, published in Cohen 1971a) on individuals in vervet monkey groups. It is too easy, and inadequate, to say that family ties, or extended family ties, explain these data. There is no precise way to know just how much such would-be explanations do explain, and how much they cannot explain. I prefer a simple admission of ignorance.

At least, by formulating quantitatively what is meant by 'randomness' and generating a set of precise expectations, the simple model of group composition offered here tells an observer when he should be surprised by his observations and when not. The model makes it possible to be certain which frequencies of group composition deviate markedly from random expectations, and to measure the direction and magnitude of the deviations.

Concluding Comment

Sometimes, simple models provide a complete account of the data. Then the models assure the observer that his observations are an orderly part of a larger pattern for which no complicated explanations need be invoked. The distribution of group sizes among orang-utans is an example.

Sometimes, simple models fail to describe adequately important parts of the data. Such cases challenge observers to identify and assess quantitatively the causal roots of the unexplained phenomena, while they challenge modelers to incorporate these causal hints in more sophisticated and successful 'simple' concepts. Such is the case of group composition among orang-utans.

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REFERENCES

- Altmann, S. A. (1965). Mathematical models of random subgroup formation. *Am. Zool.*, **5**, 420.
- Cohen, A. C. (1960). Estimating the parameter in a conditional Poisson distribution. *Biometrics*, **16**, 203-211.
- Cohen, J. E. (1971a). *Casual Groups of Monkeys and Men: Stochastic Models of Elemental Social Systems*. Cambridge, Mass.: Harvard University Press; London: Oxford University Press.
- Cohen, J. E. (1971b). Social grouping and troop size in yellow baboons. *Proc. Third Internat. Cong. Primatol.*, **3**, 58-64. Basel: S. Karger.
- Cohen, J. E. (1972a). Markov population processes as models of primate social and population dynamics. *Theoret. Population Biol.*, **3**, 119-134.
- Cohen, J. E. (1972b). Aping monkeys with mathematics. In: *Functional and Evolutionary Biology of the Primates* (Ed. by R. H. Tuttle), pp. 415-436. Chicago: Aldine-Atherton.
- Coleman, J. S. (1964). *Introduction to Mathematical Sociology*. New York: Free Press.
- Crook, J. H. & Gartlan, J. S. (1966). Evolution of primate societies. *Nature, Lond.*, **210**, 1200-1203.
- Goodman, L. A. (1964). Mathematical methods for the study of systems of groups. *Am. J. Sociol.*, **70**, 170-192.
- Lumsden, W. H. R. (1951). The night resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda; a study in relation to the epidemiology of sylvan yellow fever. *J. Anim. Ecol.*, **20**, 11-30.
- Mackinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.*, **22**, 3-74.
- Struhsaker, T. T. (1965). Behavior of the vervet monkey (*Cercopithecus aethiops*). Ph.D. dissertation, University of California, Berkeley.

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