BABOON PROGRESSIONS: ORDER OR CHAOS?
A STUDY OF ONE-DIMENSIONAL GROUP GEOMETRY

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Abstract. Baboon progressions were sampled in Africa during 1963–72. Contrary to numerous speculations, there was no invariable progression order, either by individual or by age-sex class. Indeed, most progression orders were essentially random. In the few deviant cases, usually in dangerous situations, juveniles and adult males were over-represented in the front third, adult males in the last third. Small infants were usually next to their mother, large ones next to each other. Deviations probably result primarily from residual effects of pre-progression social groupings, sometimes combined with differential roles in group co-ordination, and shifts in position, including male peripheralization, when baboons are faced with danger. Statistical techniques for analysis of group geometry are discussed. Some are insensitive to subtle spatial patterns.

Introduction

As baboons move from sleeping grove to foraging ground (or in general as they go from one major activity area to another) they often progress in an elongated formation, which in extreme form becomes a single file. Baboon progression orders are of particular interest, not only because they exhibit intragroup spatial relations in relatively simple form, but also because of a claim in the literature that baboons progress in a particular order, and that this order is of adaptive significance as an anti-predator mechanism.

Numerous progressions of yellow baboons (*Papio cynocephalus*) have been observed and recorded by us during a series of field studies, carried out in East Africa since 1963 (Fig. 1). The spatial structure of these progressions has been analysed, and provides a case history for the study of adaptive group geometry.

Previous Studies

On the basis of his observations on baboons in Kenya, DeVore (1964 and elsewhere) has maintained that the baboons of a group invariably progress in a particular order, with dominant males, adult females, and infants in the centre, and with subordinate males and juveniles in the front and back.

'A baboon troop that is in or under trees seems to have no particular organization, but when the troop moves out onto the open plains, a clear order of progression appears. Out in front of the troop move the boldest troop members—the less dominant adult males and the older juvenile males ... Following

them are other members of the troop's periphery, pregnant and estrus adult females and juveniles. Next, in the center, comes the nucleus of dominant adult males, females with infants, and young juveniles. The rear of the troop is a mirror image of its front, with adults and older juveniles following the nucleus and more adult males at the end. This order of progression is invariably followed when the troop is moving rapidly from one feeding area to another during the day, and to its sleeping trees at dusk ...' (DeVore & Washburn 1963).

DeVore & Washburn (1963) have speculated that this progression order is adaptive for a terrestrial primate, in that adult males (the class of individuals best able to defend themselves and others) are thereby placed in the most exposed positions, whereas mothers and young are safe in the centre.

'The arrangement of the troop members when they are moving insures maximum protection for the infants and juveniles in the center of the troop. An approaching predator would first encounter the adult males on the troop's periphery, and then the adult males in the center, before it could reach defenseless troop members in the center.'

The progression is sometimes described as a two-dimensional formation, with subordinate males at the sides as well (e.g. DeVore 1964; Hall & DeVore 1965).

This hypothetical progression order has been described many times by DeVore (e.g. Devore 1962, 1964, 1965; DeVore & Washburn 1960,

1963; Washburn & DeVore 1962; Eimerl & DeVore 1965; Hall & DeVore 1965; DeVore et al. 1971) and has become an established part of the literature (e.g. Pfeiffer 1969; Lasker 1973). It can be described, without exaggeration, as the most widely known claim for an adaptive group geometry that has been made for any animal. Yet surprisingly, no supporting data giving the order of individuals in even one actual baboon progression were ever published to substantiate it.

If this claim is interpreted literally, it is certainly false for other baboon groups that have been studied (Rowell 1966; Altmann & Altmann 1970 : 188; Stoltz & Saayman 1970); yet it may be a reasonably accurate description of a tendency, which might be strong or weak, and which would show up in statistically significant deviations from a merely random ordering. If so, it may be revealing to examine actual progression orders and to search for patterns in them. If there are deviations from reasonable, simple hypotheses about the system, the pattern of these deviations can be used to indicate the direction that a more adequate hypothesis would have to take.

DeVore has described the deployment of baboons at other times as well:

'At rest, the troop tends to keep much the same order it had on the march. The dominant males, the females and the infants are still in the center, but the juveniles are now romping through the troop or playing together at the edge of it. On the offensive (when faced with a predator), the dominant males emerge from the heart of the troop and take positions out in front, where they lead the other males in action against predator while the females and young retreat' (Eimerl & DeVore 1965 : 139).

The idea that monkeys progress in a regular order is not new. In 1824 the Rev. W. Bingley wrote:

'Some naturalists have been credulous enough to believe that they form a sort of republic, in which a great deal of subordination is kept up; that they always travel in a regular order, conducted by chiefs, the strongest and most experienced animals of their troop; and that, on these occasions, some of the largest monkeys are likewise placed in the rear, the sound of whose voices immediately silences that of any of the others which happen to be too noisy' (quoted in Zuckerman 1932).

However, the immediate predecessor of DeVore's claim is a series of papers on the Japanese macaque, *Macaca fuscata*, published by members of the Japan Monkey Centre, according to whom provisionised monkeys on Mt. Takasaki are deployed on the feeding grounds in concentric rings, with centrally located dominant males, along with adult females and young, and with peripheral subdominant and subordinate males (Itani 1954). DeVore's hypothetical baboon progression is, in effect, a stretched out version of that kind of arrangement (Hall & DeVore 1965), an interpretation that is implicit in Itani's own description of progression orders in Japanese macaques. Indeed, Rowell (1972) has suggested that DeVore's results are an artifact of just such artificial feeding, which is, unfortunately, a common practice in Nairobi National Park, where DeVore's study was conducted.

Stoltz & Saayman (1970) were unable to confirm the existence of definite progression orders in chacma baboons that they observed in the Northern Transvaal of South Africa. They write:

'Clearly defined formations of this nature were not observed in the present study. Under these conditions, where the majority of movements occurred when the troop foraged widely scattered through the bush, two observers, keeping in close radio and visual contact, were unable to formulate meaningful conclusions concerning the spatial relationships of the various classes of baboon with reference to the dominant and ... (subordinate) males. There was a tendency, however, for mothers with infants to remain in the vicinity of the dominant males and direct observation of troops as well as spoor counts of troops crossing open ground supported this impression.'

During 17 days of 1971, Rhine (1975) sampled progression orders in Amboseli baboons. Rhine's results may be summarized as follows. (1) There was a very slight tendency for individuals to occupy similar ordinal positions from one progression sample to another, even when the samples that were compared were at least 1 h apart, with one in the morning and one in the afternoon. But the correlation ranged from − 0·64 to 0·60, and the median correlation coefficient was only 0·19, i.e. sufficient to account for less than 4 % of the variance. (2) Positions in progression samples that were taken close

together were usually positively correlated, though about one quarter of 45 non-independent pairs of samples taken within 40 min of each other were negatively correlated. (3) Adult males tended to be near the front or back of progressions. (4) The two most dominant individuals were more often near the front, the more subordinate ones more often near the rear. (5) Riding black (i.e. the youngest) infants, and hence their mothers, were spread more or less equally across progression positions, except for a somewhat lower frequency in the first and last three positions. (6) Subadult males were biased toward the front, juveniles toward the centre. (7) The region of the group occupied by members of various age-sex classes showed no obvious relationship to type of formation (flank, elliptical file, single file, or mixed) or type of vegetation (open, bush, or mixed). (8) When approaching a waterhole, adult males shifted forward, whereas subadult males and mothers with black infants shifted to the rear: the formation was then more likely to be a neat file than at other times. Rhine points out that in data on anubis baboons from two other studies, Rowell's (1969) in Queen Elizabeth Park, Uganda, and Harding's (1973) near Gilgil, Kenya, some of these same trends can be seen, namely, over-representation of adult males in the front and rear sections, particularly in the very first and last positions, a bias of subadult males to the front and away from the rear sections, an over-representation of juveniles in the centre, and a fairly uniform distribution of black infants.

Because Rhine's Amboseli study is, more than any other, comparable to that presented here, a résumé of similarities and differences in approach, results, and interpretation is included in the Discussion section.

Rhine & Owens (1972) observed anubis baboons in Gombe National Park, Tanzania. On 20 occasions, they observed the portion of 'Camp Troop' that came into the clearing around the camp, an area in which chimps and, until recently, baboons were fed on bananas in a 'banana trench'. Typically, some baboons passed the clearing in the nearby vegetation without ever coming into sight of the observer, and thus these results are not directly comparable with those reported here. A number of interesting quantitative data are presented, but in most cases, no expected values are given. Some of them would provide a challenge to someone with a knowledge of combinatorial probability (e.g. frequency with which at least

one animal other than a black infant's mother left camp after the last black infant; median number of individuals and of adult males present when the first black infant arrived in the clearing; proportion of cases in which at least one adult male arrived before a black infant). In the absence of the appropriate expected values, there is no way to know whether, or in what direction, such observed results differ from chance.

Rhine & Owens (1972) single out two of their results as being consistent with the idea of adult males as protectors. First, according to them, 'black infants were closer than 3-year-olds to adult females'. (Presumably, 'closer on the average', or something similar, is implied, not that they were always closer.) Actually, the method that was used for recording distances, a one-zero scoring method, does not permit such conclusion to be drawn (J. Altmann 1974); rather, their data (their Fig. 2) are consistent with the more circuitous claim that for juveniles, compared with infants, there is a smaller proportion of 1 min intervals during which they came within 10 feet (3·04 m) of an adult male at least once, and a larger proportion of 1 min intervals during which they were more than 10 feet from an adult male at least once. The significance of this observation is obscure. Second, Rhine & Owens indicate that adult males were first to enter the clearing more often than expected from troop composition. According to Rhine & Owens, unpublished observations by Harding on anubis baboons in open grassland indicate that 'black infants were almost equally spread from front to back in 59 progressions', a difference that they attribute to 'a more relaxed setting', i.e. a place where danger from predators was minimal.

Rowell (1969) sampled and analysed progression orders in anubis baboons that she observed in the Ishasha River Flats of Queen Elizabeth National Park, Uganda:

> 'Twenty good counts each of S and V troops were analyzed for any pattern in order of movement. First and last animals in each progression and the proportion of the various (age-sex) classes in successive blocks of five positions were checked using χ^2 and a null hypothesis of random distribution of classes in the progression . . .

No position was exclusively occupied by any one class of animal. There was usually an adult male in the lead (90% of progressions in V group, 45% in S group), and one at the

rear (55 % in V group, 30 % in S group), and adult males were significantly more frequent in the first block of 5 positions in the progression ($P < 0.001$). The only other significant difference in distribution from random was an excess of small (walking) juveniles in the middle of both troops, and of adults at front and rear.'

My bracketed inserts above are from Rowell's Fig. 1. Her discussion continues with a résumé of other, apparently non-significant, differences in positions.

Kummer (1968) has described the spatial deployment of hamadryas baboons (*Papio hamadryas*):

'In the resting unit the females will sit more or less in a circle around their (harem) leaders ... As soon as the troop begins to move, however ... the females, instead of surrounding the leader, keep on his safest side. They either line themsleves up between their leader and a previously disregarded neighboring male, or they form a line directed towards the center of the troop. Very frequently, two units will walk in a line in which the males take the front and rear; or if the column is moving abreast of the direction of march, the males march in the wings. ... The frequency with which adult and subadult males appear at the front of their columns is twice that which would be expected under conditions of random mixing. On the other hand, these two classes were found bringing up the rear with a frequency equal to chance. In parties in which there are only two males, the marching order is less flexible and the front and rear are almost always taken by two leaders.'

Other literature on primate spatial relationships, including progression orders, has recently been reviewed by Wilson (1972).

Methods

Subjects

The animals that we studied are wild yellow baboons (*Papio cynocephalus*) living in the Maasai-Amboseli Game Reserve (now Amboseli National Park) of southern Kenya. The progression data analysed here were obtained during several field studies (1963–64, 1969, 1971–72). Most of the data come from observations on groups that have been the focus of several research projects in Amboseli. These have been supplemented by data from several other groups in the same study area and by a few observations on anubis baboons at other study sites. The observations were made by me and by several collaborating investigators: Jeanne Altmann, Joel Cohen, Glenn Hausfater, Sue Ann McCuskey and Montgomery Slatkin.

The Amboseli baboon population and habitat as of 1963–64 have been described elsewhere (Altmann & Altmann 1970). The area is primarily short-grass savannah, with acacias as the only common trees. Since our first study, the area had undergone marked changes, primarily as a result of long-term trends in rainfall. The plant association has been rapidly changing into a xeromorphic, halophytic community (Western 1973; Western & Van Praet 1973).

Observations

Any displacement of a group's centre of mass could be regarded as a group progression (e.g. Rhine 1975). The progressions that were sampled for this study were elongated file formations, either literally single file or more elliptical file formations, but in every case, ones in which there was a distinct order of individuals from front to back. Baboons in progressions were censused at opportune times during the course of several projects. With experience, we learned to anticipate their route of progression. From a position ahead of and to the side of the anticipated route, we selected a line of sight that was as free as possible of obstructing vegetation. We picked out some small visual marker, such as a rock or the edge of a distant tree, that would clearly fix the line of sight or 'counting point'. Then, as each individual in turn walked past this imaginary line, its age-sex class was recorded. Whenever two individuals were close together as they passed the counting point, the order was determined 'horse race style', i.e. depending on whose nares crossed first. If an individual turned back across the counting point, then crossed it a second time, it was counted as being in its second position. Whenever possible, individual identifications were made. Several kinds of additional data that will not be used here (e.g. wounds, condition of females' sexual skin and paracallosum) were also obtained at the time. During many of these censuses, a second observer not only confirmed observations but also continued to observe individuals that were inadequately observed by the primary observer, who remained with eyes fixed on the counting point so as not to miss the next individual. Observations were facilitated by using 7x, 35

mm (or 10x, 50 mm) binoculars, propped in position so that the observer could keep continuous watch on the counting point. Data were usually dictated into a portable cassette recorder, thereby eliminating any need to look down to write.

Methods of Analysis

The procedure of our analysis was to formulate a series of simple, reasonable, and testable hypotheses or models about progression orders, then to use these models to predict characteristics of progressions. For each hypothesis, we asked, what type of data is required to answer the question and what kind of analysis is appropriate? Each kind of statistical analysis that was used required certain types of data, and these data had to meet specified criteria of completeness and accuracy, as will be indicated below. Many censuses were not completed because conditions proved inadequate, for any of a variety of reasons, e.g. bunching of the animals, movement of individuals behind obstructing vegetation or in an unexpected direction. Such partial censuses were not used here. For each analysis, we used all and just the censuses that met the indicated requirements. The samples and their criteria are summarized in Table I.

A variety of procedures was used, depending in each case on the nature of the hypothesis to be tested. Some of the methods are well established in the literature on statistical inference. Others are not well-known or are original. Because the geometry of groups is now being studied in several animals, the methods of analysis that were used in this study may be of interest to others. They are summarized in the Appendix.

Results

1. Invariant Orders

We begin by considering DeVore's hypothesis that when a group of baboons moves from one activity site to another, they do so in a fixed order of progression. In the most extreme version of this hypothesis, it would be the case that every individual's position in the progression would be completely specified, as in a military formation. In the least extreme version, position would be fixed only to major sections of the file (e.g. front, middle, rear) and only by gross age-sex

Table I. Criteria and Sizes of Samples

Sample	Criteria	Sample size
I.	Every adult must be included in order and be classified as male or female. Adult composition of group must be known independently	76
II.	Every adult male must be included in order and be identified by name. The number of individuals in the sample must agree with the number in the group, which must be known independently. There must be no unresolvable discrepancy in age-sex classification. (This sample is a subset of Sample I)	43
III.	Every individual must be classifiable as adult male, adult female, juvenile, infant-1, or infant-2. For groups whose composition is independently known, the number in the sample total must agree with the number in the group. No unresolvable discrepancy in age-sex classification. For groups whose composition is not independently known, the error factor (cf. Altmann & Altmann 1970) must be $(+ 1, - 1)$ or better, and the age-sex determination must have been rated as good, very good, or excellent. The ordinal position (96 cases) or sector position (97 cases) of every individual must be known	97
IV.	The dominance rank of all adult males in the group must be known. Every adult male must be included in the sample, his position must be recorded accurately enough to determine whether he was in the front, centre, or rear third of the group, and he must be identified. The sample total must agree with the known group total	24
V.	Same criteria as in Sample IV, but for adult females. Same censuses used in both	24
VI.	The dominance rank of all adult males in the group must be known, all must be included in the sample, and their order in the progression relative to each other must be recorded. (Samples IV and VI have 23 samples in common)	24
VII.	Same criteria as in Sample VI, but for adult females. Same samples used in both	24

classes (e.g. adult male, adult female, etc.). Of course, the former implies the latter (though not vice versa). Therefore, if the latter is false, so must the former be.

Hypothesis 1: *There is an invariant progression order in a group of baboons, at least among major age-sex classes.*

This hypothesis can be disproved by a single counter-example (Method 1, Appendix). We have observed many such examples (Table II).

In none of the baboon groups that we have studied is there a fixed progression order, either by individual or by age-sex class. Indeed, we have seen members of virtually every age-sex class at every place in the group, including adult females with small, clinging infants in the front and rear of the group. When one examines actual progression orders, it quickly becomes apparent that the ordering relationships, whatever they may be, are much more subtle. The

Table II. Examples of Progression Orders That Are Contrary to Hypothesis 1. Only a Small Selection of the Available Variants are Listed Here. Progressions 1–4, 6, 7, 11, 12, 14–20 are Examples of Progressions in Which an Adult Female is the First or Last Individual. Infants and Juveniles Were Members of 12 of These Progressions (Nos. 5, 8, 9, 11–19); The Smaller Infants (i_1's) Were Riding on Their Mother's Back or Belly. M = Adult Male, F = Adult Female, j = juvenile, i_1 = Small Infant, i_2 = Large Infant, rv = Riding on Ventrum of Adult, rd = Riding on Dorsum of Preceding Adult

No.	Group	Date, time	Order (front to back)
1	Alto	24 Jul. 69, 1023	F–M–F–j–F–j–j–F–F–F–j–M–j–F–F–F–j–j–i_2–j–i_2–i_2–M–i_2–F–i_1(rv)–j–i_2–i_2—M–F–M–F–M–M–M–F
2	Alto	24 Jul. 69, 1244	F–M–j–j–F–j–F–M–i_2–F–F–j–j–j–M–i_2–j–F–j–M–F–M–j–i_2–i_2–F–i_2–F–i_2–F–M–F–F–i_1(rv)–M–M
3	Alto	25 Jul. 69, 1127	M–F–j–j–F–i_2–F–j–j–F–j–i_2–j–F–j–M–M–M–i_2–i_2–j–i_2–F–F–i_2–j–F–i_1(rv)–M–F–M–M–F–i_2–j–M–F
4	Alto	14 Sep. 69, 1045	F–M–F–M–M–j–j–j–j–F–F–j–M–j–j–j–F–F–i_2–j–i_2–i_2–F–F–F–i_1(rv)–F–i_2–j–F–i_1–(rv)–M–F–M–F–M–M
5	Hook	24 Aug. 69, 0804	M–M–F–i_2–i_2–j–j–F–j–F–M–F–j–i_2–j–j–j–i_2–F–j–M–F–M–j–j
6	Kijiko	24 Jul. 69, 0945	M–F–M–F–F–i_2–F–i_2–i_2–i_2–i_1–F–i_1(rv)–j–F–F–j–F
7	Kijiko	26 Jul. 69, 1551	F–j–M–F–F–M–F–F–j–M–i_2–j–F–i_1–j–F–i_1(rv)–F
8	Kikijo	8 Aug. 69, 1355	M–M–i_1–i_2–M–F–F–F–F–i_1(rv)–j–F–F–j–i_2–i_2–F–i_2
9	Kijiko	1 Sept. 69, 1607	M–F–F–j–M–i_2–i_2–i_2–j–F–F–i_2–i_2–F–F–M–F–i_1(rv)
10	Spoon	11 Jul. 69, 1715	M–F–M–F–i_2–j–F–i_2–M–j–F–j–M–j–j–j–F–i_2–M–j–j
11	Spoon	25 Jul. 69, 1623	F–j–F–M–F–M–F–i_2–i_2–i_2–i_1–i_2–F–j–F–i_1–F–M–j
12	Tembo	7 Aug. 69, 1700	F–M–j–F–F–F–j–j–F–j–F–i_1–j–i_2–j–M–F–i_2–j
13	Alto	19 Aug. 71, 1023	j–F–j–M–i_2–i_2–F–j–j–F–j–F–M–j–M–j–F–i_1(rv)–F–i_1(rv)–i_2–F–i_2–j–M–F–j–F–F–F–M–M–F–i_1(rv)–M
14	Alto	1 Nov. 71, 1207	F–F–M–F–i_1(rv)–F–M–i_2–j–j–j–j–M–i_2–i_2–M–j–M–F–i_2–F–j–M–F–F–i_1(rv)–M–F–j
15	Hightail	20 Aug. 71, 1817	F–j–F–i_2–i_2–F–i_2–F–F–i_2–j–M–F–i_1(rv)
16	Hightail	25 Jun. 72, 1134	F–j–j–F–i_1(rv)–M–M–j–j
17	Hightail	9 Jul. 72, 1047	F–M–j–F–i_1(rv)–j–j–j–j
18	Hook	5 Aug. 72, 1533	j–F–j–M–j–j–i_2–F–F–i_1(rv)–F–j–M–F–F–F–j–F–i_1–i_2–M–M–F–i_1(rv)–F
19	M G	5 Jun. 64, 1021	j–F–F–j–F–M–F–j–j–F–M–j–j–F–j–F–j–F–j–F–i_1(rv)–j–F–M–F–j–j–F–j–F–F–M–i_2–F–i_1(rv)–F–M–M–F
20	Small	29 Mar. 64, 0743	F–M–j–F–j–j–j–F–i_1(rv)–F–i_1(rd)–M–j–M–j–i_2–F–F

rest of this paper will be devoted to a search for these relationships.

2. Sectional Trends

Let us state a weaker form of the first hypothesis, for which it may be possible to provide a stronger defence:

> Hypothesis 2: *Dominant males, adult females and infants tend to be in the centre section of progressions, whereas subordinate males and juveniles tend to be in the front and rear sections, more often than would be expected if position is independent of age-sex class.*

I shall begin a test of this hypothesis by examining the distribution of age-sex classes among the three sections of progressions to see whether class and section are independent. Then, in Part 3, below, I shall examine the specific relationship between male dominance rank and section.

Each progression was divided into three sections, front, centre, and rear, as described below, and the numbers of individuals of each class that were in each section were tallied. Because the hypothesis as stated above only suggests the direction of deviation from an independent positioning but does not indicate the magnitude of the deviations, expected values were obtained from the assumption of independence between section and age-sex class (Method 2 in Appendix). The observed values were tested for goodness-of-fit by means of Pearson's χ^2. The age-sex classes that were used here and elsewhere in this paper are as follows: infant-1, 0 to 0·5 year; infant-2, 0·5 to 1 year; juvenile, 1 year–adulthood; adult female, over 4 years; adult male, over 6 years. Field characteristics that were used to distinguish these classes have been published in our monograph *Baboon Ecology*, Table 1 by J. Altmann et al. 1977. For a few youngsters of one group in 1963–64, small discrepancies from the above classes resulted from our former practice of assigning January 1 as a uniform class birthday (cf. Table IV in Altmann & Altmann 1970).

The three sections of a progression were taken to be the first, middle and last thirds of the group whenever the number of individuals could be evenly divided by three. If there was a remainder of one, the middle section was taken to include one more than each end section. If there was a remainder of two, each end section included one more than the centre. Thus, a group of 30 individuals would be partitioned as 10/10/10, a group of 31 as 10/11/10, and a group of 29 as 10/9/10. In each case, expected values were

calculated on the basis of the actual size of each section, as well as the number of group members in each age-sex class at the time of the progression. The data set that was used consists of all censuses that are believed to be complete and in which the age-sex class of every individual is known to the accuracy that is indicated by the definitions of the classes used (Sample III, Table I).

In total, 96 progression orders in yellow baboons in Amboseli and one in a group of anubis baboons were analysed for independence between age-sex class and section. Of these, significant deviations at the 0·05 level were obtained in 12 cases, including the anubis (Table III). At this fiducial level, one out of 20 cases, or about five out of 97, can be expected to show pseudo-significance, i.e. will exceed this level by chance alone. Thus, while most of the observed progressions did not deviate significantly from what would be expected if members of each age-sex class positioned themselves without regard to the section of the progression order, a small number probably did.

The 12 deviant progression orders were examined in two ways, first to see whether there is a consistent pattern of deviations, and second, to see whether there was anything special about the circumstances under which significant deviations occurred. Patterns of deviations were searched for by calculating, for each age-sex class of each deviant progression, the percentage deviation of the observed value from the value expected under the hypothesis of independence between age-sex class and file section. The results, shown in Table III, indicate that even in these 12 deviant progressions, no one age-sex class was invariably responsible for the deviations. The most frequent sources of deviation were (1) large infants, which were often under-represented in the front third of the group (in 10 out of the 12 deviant cases), (2) adult males, which were often under-represented in the centre of the group (10 of the 12 deviant cases), though they were over-represented in the front and rear sections only six times and seven times respectively, (3) juveniles, which were often under-represented in the rear third (10 of 12 deviant cases), but over-represented in the front third (eight of 12 deviant cases), and (4) adult females, which were often under-represented in the front but over-represented in the centre of the group (8 of 12 deviant cases each). This last result is consistent with Hypothesis 2, but it must be remembered that these are only eight

Table III. Age-sex Class Distribution in Front, Centre, and Rear Sections in the 12 Deviant Progressions. For Each Census, Two Sets of Figures Are Given, the Observed Numbers of Individuals (obs.) and the Percentage Deviations (%dev.) of the Observed Numbers of Individuals From the Number Expected if Location Were Independent of Class. Census 97 Was Taken on Anubis Baboons in Lake Manyara National Park, Tanzania. All Others Are From Yellow Baboons in Amboseli. Symbols: ♂ = Adult Male, ♀ = Adult Female, j = Juvenile, i_2 = Infant$_2$, i_1 = Infant$_1$

Census	Date, Time		Front ♂	♀	j	i_2	i_1	Centre ♂	♀	j	i_2	i_1	Rear ♂	♀	j	i_2	i_1	χ^2
7	11 Apr. 64, 1245	obs.	2	8	4	0	0	0	6	8	0	0	6	4	2	2	0	16·333
		%dev.	−25	33	−14	100	—	−100	0	72	−100	—	126	33	−57	203	0	
17	25 Jun. 64, 1158	obs.	2	2	8	0	1	0	8	4	0	1	4	7	0	1	1	17·647
		%dev.	0	−65	100	100	0	−100	41	0	−100	0	100	−24	−100	203	0	
20	23 Jul. 64, 1728	obs.	0	5	6	1	0	0	5	5	0	2	4	6	1	0	1	15·625
		%dev.	−100	−6	50	203	−100	−100	6	25	100	100	201	12	−75	−100	0	
36	16 Aug. 69, 0955	obs.	3	3	0	0	0	0	3	1	2	1	0	2	4	0	0	17·518
		%dev.	219	19	−100	−100	−100	−100	2	−46	174	178	−100	21	155	−100	−100	
41	17 Jul. 69, 1000	obs.	1	4	0	2	0	1	2	5	0	0	3	2	0	2	0	14·036
		%dev.	37	57	−100	57	—	−45	−31	176	−100	—	89	−21	100	57	—	
50	8 Aug. 71, 1343	obs.	5	3	4	0	0	2	4	3	0	2	0	5	2	4	1	16·285
		%dev.	108	−27	30	−100	−100	−9	6	6	−100	113	−100	22	−35	192	−2	
63	16 Sept. 71, 1129	obs.	4	2	4	0	1	0	2	2	5	1	3	7	1	0	0	21·517
		%dev.	67	−47	67	−100	47	−100	−42	−8	220	61	25	85	−58	−100	−100	
87	20 Feb. 72, 1823	obs.	3	2	6	0	0	2	7	1	1	0	5	3	1	2	0	13·149
		%dev.	10	−50	126	−100	—	40	75	−62	0	—	50	−25	−62	100	—	
88	9 Apr. 72, 1320	obs.	5	2	4	0	0	3	5	5	0	0	1	5	1	4	0	13·830
		%dev.	62	51	67	−100	—	7	33	19	100	—	68	21	58	192	—	
94	14 Jun. 72, 1759	obs.	7	6	6	3	0	1	8	5	6	1	6	6	2	1	2	16·251
		%dev.	9	−11	36	−11	−100	−84	24	19	86	4	−11	−11	−54	−70	98	
96	23 Nov. 71, 0829	obs.	1	3	0	0	0	0	1	1	2	0	0	0	4	0	0	14·699
		%dev.	203	126	−100	−100	—	100	−25	−40	203	—	−100	−100	141	100	—	
97	27 Dec. 71, 1122	obs.	3	3	13	2	1	5	6	5	2	4	4	7	3	6	2	15·980
		%dev.	−30	−43	89	−39	−56	30	9	30	−42	67	−6	33	−56	83	−13	
Total		obs.	36	43	55	8	3	15	57	42	18	12	41	54	21	22	7	41·5247

cases out of 97 in the sample. Another way to look at these deviations is in terms of their magnitude: the 10 cells of Table III with the largest percentage deviations were all due to adult males (three cases) or large infants (seven cases).

Next the data from these 12 deviant cases were combined, as if each crossing of the line of sight was an independent replication or sample from an infinitely large population, and again, a chi-square test of independence was carried out. If the above-mentioned deviations are the result of small-sample fluctuations, they would tend to cancel each other when results are pooled. Despite pooling, the combined table was highly significant: $P(\chi^2 = 41\cdot52) < 0\cdot005$. Again, percentage deviations were calculated. The results (observed values and percentage deviations from expected values) are given at the bottom of Table III. All of the above-mentioned discrepancies continued to hold.

We have checked our field notes on these 12 deviant progressions in order to see whether there was anything special about the circumstances under which they occurred. Three cases (numbers 36, 41 and 50) occurred when the group withdrew from the proximity of Maasai tribesmen. Three others occurred when the censused group was in close proximity to another group and either moving toward them (number 17) or avoiding them (numbers 7 and 96). In two cases (numbers 87 and 94), the group was moving to their sleeping grove in the evening. In one (number 20), they moved rapidly away after approaching a grove that they had almost adopted the previous evening; this progression, late in the afternoon, included the longest half-hour progression observed in the 1963–64 study (Altmann & Altmann 1970). In one case (number 63), the group was moving into a waterhole depression, where they drank. For the remaining two cases (numbers 88 and 97), which included the one deviant anubis sample (number 97), no special contextual events are indicated; these are the only two cases among the 12 deviant progressions in which adult males were not under-represented in the centre. In short, progressions in which adult males were over-represented in the peripheral portions and under-represented in the central third of the group, were almost always ones in which the group was in an actually or potentially dangerous situation (cf. Altmann & Altmann 1970).

3. Male Ranks and Regions

Of course, even a random distribution of adult males among the front, centre, and rear sections of the group would not preclude the possibility that dominant adult males tend to be in the centre of the group whereas subordinate males tend to be in the two peripheral sections. In order to examine the relationship between male dominance rank and position in group progressions, we have utilized data from a group in which male dominance was the focus of an extensive study (Hausfater 1975). The dominance rank of every male at the time of every progression recorded during a period of 14 months is known. For most days the dominance hierarchy among the adult males in the group was linear. On those days on which a male's status was indeterminate by Hausfater's criteria, which usually meant that he was changing rank, the male's rank immediately after his indeterminate period was used in this analysis. For each suitable progression order, the entire group was divided into front, centre, and rear thirds, as before, and the dominance rank of every male in each of these three sections was tabulated, using 1 for the rank of the most dominant male, and so forth. Twenty-four progression censuses that met the necessary sampling criteria (Sample IV, Table I) were available for analysis. Four of the progression orders used in this analysis were observed on days when one or two males were temporarily absent from the group, but did not remain away long enough for Hausfater to consider them as having emigrated. In these four cases, I 'closed up ranks', so that all males that were present were rank ordered consecutively, 1, 2, 3, etc.

Before examining effects of rank, let us look at the distribution of those males among the three major sections: front, centre and rear thirds of the progressions. When the data on adult males in the 24 censuses are combined, as if they represented repeated and independent samples from a common underlying population (column totals, Table IV), they indicate that in 75 (43%) of the observations on adult males, they were progressing in the front third, in 36 (20%) they were in the middle third, and in 63 (36%), in the rear third of the group. This result deviates markedly from what would be expected if males were equally distributed among sections of the group : $P(\chi^2 = 13\cdot759,\ df = 2) < 0\cdot01$. Thus, the deviation in this combined sample is like that noted in Section 2 above, namely,

adult males as a class tended to be under-represented in the central third of the group.

Now, what about the ranks of these males? Since Hypothesis 2 does not indicate the expected magnitude of the hypothetical tendency of dominant males to be central, and of sub-ordinate males to be peripheral, expected values were obtained from the assumption of independence between male rank and position. If males' choice of front, centre, or rear thirds of group progressions is independent of their dominance ranks, then the males in each of these three sections can be considered to have been drawn from a common population, and will differ in mean rank only as a result of small sample fluctuations. This hypothetical equality of rank is contrary to Hypothesis 2, and can be stated explicitly:

Hypothesis 3: *The mean dominance ranks of adult males in the front, centre, and rear thirds of group progressions are equal.*

If one combines all 24 censuses, the mean dominance ranks of the adult males were 3·67, 4·25, and 4·70 in the front, centre and rear thirds, respectively. This result is clearly at variance with the hypothesis that the most dominant males are central. Are these observed differences in mean ranks statistically significant? Differences between these three means were examined by a one-way analysis of variance, fixed effects model (Method 4, Appendix). The between-section sum of squares (S_1) was 124·58 with 2 df. The within-section mean square was 4·63, based on 171 df. The latter is the true variance of the sample population, not an estimate, because the distribution of rank numbers is determined by the number of adult

males in the group. Consequently, the ratio S_1/σ^2 is distributed as $\chi^2{}_2$. The value $124·58/4·63 = 31·78$ is significant at the 0·05 level and we conclude that there are significant differences among mean ranks of adult males in the three sections.

Because there appears to be a secular increase in mean rank number from front to back, we tested mean differences for adjacent sections. Between the front and centre sections, the difference in mean rank of adult males was 0·58. The standard error of this difference is 5·25 and thus $t_{171} = 0·11$ (two-tailed) which is not significant at the 0·05 level. Between the centre and rear sections, the difference in mean rank of adult males was 0·45. The standard error of this difference is 5·41 and thus $t_{171} = 0·08$, which is not significant. Finally, we examined the difference in mean rank between the adult males in the front and rear sections, which is the largest difference, namely, 1·03 ranks. The standard error of this difference is 4·426, giving $t_{171} = 0·233$, which is not significant. Apparently, the discrepancies between the section means and the population means are sufficiently small that no single paired comparison appears significant, even though the aggregate of the deviations is significant. A graphic summary of sectional differences in male dominance rank is presented in Fig. 2.

In this pooled sample, the observed increase in mean rank of adult males from front to back

Table IV. Frequency with Which Males of Each Rank Progressed in the Front, Centre, or Rear Thirds of the Group. Based on 24 Censuses in Sample IV. S = Significant at 0·05 Level When Tested Against Distribution in Column Totals

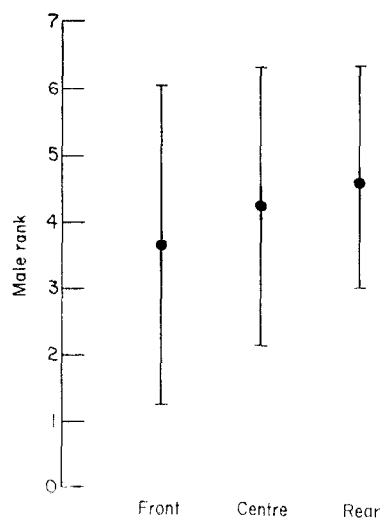| Rank	Front	Centre	Rear	χ^2	0·05 Sig.
1	17	3	4	7·590	S
2	15	7	2	8·078	S
3	11	4	9	0·240	—
4	5	7	12	4·856	—
5	10	3	11	1·403	—
6	2	4	18	16·894	S
7	9	7	6	1·826	—
8	4	1	1	1·452	—
9	2	0	0	2·640	—
Total	75	36	63		

Fig. 2. Sectional differences in adult male dominance ranks, showing means and one standard deviation on either side of the means.

in the group is small. Is it of sufficient magnitude to show up in individual progressions? Or is it possible that there are opposite differences that are cancelling each other in the pooled sample? Equality in mean dominance ranks of adult males in the three sections of individual group progressions was tested by means of the *H* test of Kruskal & Wallis (1952, 1953) (Method 4, Appendix) when adult males were present in all three sections, and by a U-test (Wilcoxon 1945, 1947; Mann & Whitney 1947) using the tables of White (1952) when one section (always the centre) was devoid of adult males. A test was carried out for each of the 24 progressions used above (Sample IV, Table I). Of these 24, only 1 (for 13 Sept 1971, 1045) showed between-section rank differences that were significant at the 0·05 level. It thus appears that male rank differences between sections are sufficiently subtle or rare that they can only occasionally be detected in individual progressions.

How variable are the individual males in contributing to the total observed differences in the number and mean rank of males in the three sections of the group? We can tabulate the frequency with which the males of each rank occupied each of the three sections (Table IV). Alternatively, we can tabulate such section distributions for individual males (Table V). Because of numerous rank changes in the course of the study period (Hausfater 1975), these two tables are not identical. From these tables it is clear that while all ranks and all individual males except one (Crest, who was in the group during only three recorded progressions) were over-represented in one or both of the peripheral sections of the group, much of the front-to-back

increase in mean rank order was the result of the idiosyncracies of two adult males: male Stubby, who was high ranking and usually in the front third of the group, and male Sinister, who was low ranking and was almost always at or near the back of the group. For no other males was there a significant deviation (0·05 level, chi-square goodness-of-fit tests, Table VI) between their distribution among the sections of the group and what would be expected from the overall distribution of adult males among sections. Much the same pattern emerges from a detailed examination of rank versus section (Table V): the only significant deviations were for the males of ranks 1 (usually male Stubby, sometimes BJ) and 2 (usually Peter, sometimes Ivan, Stubby or BJ), who usually were in the front third of the group, and the males of rank 6 (usually Sinister, sometimes Cowlick), who were usually in the rear third.

It thus appears that (1) the under-representation of adult males in the central third of these progressions was due to a tendency of virtually all males to progress in one or the other of the two peripheral sections, whereas (2) the small increase in mean rank of adult males from front to centre and from centre to rear sections of progressions was largely due to the influence of two males.

We can now summarize the significance of the findings in Parts 2 and 3 for Hypothesis 2. The speculation that dominant males tend to be central and subordinate males peripheral is contradicted by the data, which indicate that the mean dominance rank number of adult males tends to increase very slightly from the front to the back of the group and that adult males in general are under-represented in the central third of the group. The speculation that adult females tend to be centrally located received only weak support: the age-sex distribution of individuals among sections of the group was non-random in only 12 out of a sample of 97 progressions, and in these 12 deviant progressions, adult females were over-represented in the central section in eight cases, under-represented in the remaining four. In the remaining 85 cases, the distribution was indistinguishable from random.

4. Female Ranks and Regions

Among cercopithecine primates, much sexual dimorphism involves special traits of adult males, such as elongated canines, greater body size and musculature, that make them formidable

Table V. Frequency with Which Individual Adult Males Progressed in the Front, Centre, or Rear Thirds of the Group. Based on 24 Censuses of the One Group in Sample IV. S = Significant at 0·05 Level When Tested Against Distribution in Column Totals

Male	Front	Centre	Rear	χ^2	Sig.
BJ	6	1	3	1·322	—
Crest	1	1	1	0·304	—
Cowlick	7	3	12	3·225	—
Dutch	8	4	12	1·982	—
Ivan	8	7	8	1·435	—
Max	14	6	4	4·036	—
Peter	12	6	4	3·101	—
Sinister	1	4	17	17·907	S
Stubby	18	4	2	11·004	S
Totals	75	36	63		

adversaries. Not surprisingly, then, much of the literature on primate social systems has emphasized dominance in adult males. Nevertheless, there is a growing body of literature suggesting that relationships among adult females may be of greater significance in the organization of the society (Sade 1972). Females of many cercopithecine species are more stable members of the society: they seldom migrate from one group to another, and their dominance relationships are far more stable. For example, in one group of Amboseli baboons studied during 1963–64 (Altmann & Altmann 1970), there were $1·07 \times 10^{-3}$ emigrations per adult male-day, but none among the 21, then 20, adult females. In another Amboseli baboon group, studied by Hausfater during 1971–72 there was an agonistically induced change in adult male dominance rank once every 528 adult male dyad-days, on the average, but no change in 18 884 adult female dyad-days (Hausfater 1975). Female rhesus monkeys and perhaps other female primates assume a dominance status immediately below that of their mother and above that of all their older sisters (Sade 1972); the rank of the mothers may also influence that of their sons. Furthermore, we have, on several occasions, been convinced that critical decisions about the direction of group movements in Amboseli baboons were being made by adult females.

Thus, it may be worthwhile to examine the relationship between the dominance rank of adult females and their positions in group progressions. In Part 3, we tested for differences in the mean rank of adult males that occupied the three sections, front, centre, and rear. We shall now present the comparable test for adult females.

Hypothesis 4. *In progressions, the mean ranks of adult females in the front, centre, and rear thirds of the group are equal.*

We note first that this sample of 24 progressions (Sample V) differs from the larger sample analysed in Section 2 in that adult females are here under-represented rather than over-represented in the centre of the group. The numbers of occurrences of adult females in the front, centre, and rear thirds of these 24 progression samples were 81 (32%), 68 (27%), and 101 (40%), respectively. By a chi-square goodness-of-fit test to the hypothesis of equal distribution, these results are significantly deviant: $P(\chi^2 = 6·632, df = 2) < 0·05$.

The mean ranks of the adult females were very similar in these three sections: the means of ranks were 6·09, 5·32, and 5·70, for the front, centre, and rear thirds of the progressions, respectively. The possibility that these means differ significantly was tested in the same manner as in the male sample, above. The between-section sum of squares was 21·59; the variance (within-section mean square) was 9·14. Thus, $\chi^2 = 2·36$, with 2 df, which is not significant. When the 24 samples were individually analysed for sectional differences in rank, using the H test of Kruskal & Wallis (Method 4 in Appendix) only one (6 Sept 1971, 1408) was significant at the 0·05 level, which is in close agreement with the long-term expectation of about one case of pseudo-significance out of every 24 samples. We conclude that the distribution of females among the front, centre and rear thirds of these progressions is independent of their dominance ranks.

I shall now take a different tack in the search for non-random ordering principles in baboon progression orders: in what follows I shall consider the possibility that there are attractions and repulsions between a baboon and its neighbours, rather than between a baboon and certain regions of the group, as I have done above. I shall first consider class attraction (Sections 5–7), then attraction to specific individuals (Sections 8–11).

5. Classes of Adjacent Pairs

The most obvious way to analyse the relationships of individuals that progress near each other is to make up a contingency table for each censused progression, tabulating in each cell i, j the number of pairs of adjacent individuals in which the first member was in class i and the next in line was in class j. We can then test the distribution for independence.

Hypothesis 5. *The age-sex class of the individual in each position in a progression is independent of the age-sex class of the individual immediately ahead of, or immediately behind it.*

The tabulation was carried out for each of the 96 censuses of yellow baboons in Sample III (Table I).

In attempting to apply to these tables the usual test for independence between row and column attributes (Method 5, Appendix), we encountered several problems. Sample sizes were always too small: using just five classes (adult males and females, juveniles, old and young infants), there are 25 cells in each table, yet the groups were primarily in the range of 25 to 50

Table VI. Frequency Distributions of Adjacent Pairs Ordered Front to Back, by Age-sex Classes. The Table Gives Data for the 19 Pooled Samples, Based on 96 Censuses, That Were Significant at the 5% Level, and for all 96 Censuses Combined. For Each Pooled Sample, Two Sets of Figures are Given, Observed Values (obs.) and Percentage Deviations (%dev.) of the Observed Values from the Hypothesis of Independence Between the Age-sex Classes of the First and Second Individuals in Adjacent Pairs. Symbols as in Table III

Composition and group $\male\male$-$\female\female$-jj-ii_2-ii_1	No. of censuses		$\male,\male$	$\male,\female$	$\male,j$	$\male,i_2$	$\male,i_1$	$\female,\male$	$\female,\female$	$\female,j$	$\female,i_2$	$\female,i_1$	$j,\male$	$j,\female$	j,j
7-12-9-4-3 (Alto's Group)	3	obs.	4	7	6	2	0	6	9	8	4	8	6	13	8
		% dev.	13	4	24	10	100	8	27	10	3	160	20	37	17
7-11-7-6-2 (Alto's Group)	3	obs.	5	8	3	3	0	11	7	6	2	6	1	7	6
		%dev.	33	26	-28	16	100	-74	-34	14	-67	200	-76	0	31
7-11-7-5-2 (Alto's Group)	7	obs.	13	16	9	5	0	15	19	17	11	14	6	26	10
		%dev.	53	6	-7	-28	100	-0.3	-29	-0.9	-10	186	-38	52	-10
7-10-7-4-2 (Alto's Group)	4	obs.	4	14	4	4	0	12	8	7	4	8	3	11	9
		%dev.	-26	56	-36	12	-100	49	-40	-26	-26	199	-48	14	33
9-10-7-4-2 (Alto's Group)	2	obs.	4	5	7	0	0	9	4	2	2	3	3	2	4
		%dev.	-14	8	94	-100	-100	55	-31	-56	-22	133	-26	-51	27
7-17-13-2-0 (Main Group)	4	obs.	8	11	5	1	—	11	35	17	4	—	9	13	27
		%dev.	74	5	-42	-24	—	-11	-24	-26	14	—	-6	-41	52
Alto's Group, 1969	5	obs.	9	17	7	4	0	16	13	14	10	6	8	16	16
		%dev.	15	43	-30	-33	-100	29	-32	13	5	206	3	1	20
Kijiko's Group, 1969	8	obs.	4	14	1	2	1	6	22	11	8	10	3	14	5
		%dev.	56	43	-75	-46	48	10	-13	6	-16	100	3	26	10
Spoon's Group, 1969	3	obs.	1	6	5	0	0	6	1	6	6	1	2	7	4
		%dev.	-59	64	54	-100	-100	48	-84	11	61	49	-30	64	6
Tembo Group, 1969	3	obs.	0	4	4	0	0	3	3	6	3	4	3	8	4
		%dev.	-100	42	59	-100	-100	22	-55	0	22	185	45	42	-20
Alto's Group, 1971-72	26	obs.	34	72	43	21	0	69	64	52	38	46	33	77	57
		%dev.	-5	26	6	-18	-100	21	-29	-19	-7	184	-18	20	25
Hook's Group, 1971-72	7	obs.	14	22	19	1	0	20	22	17	9	13	16	23	12
		%dev.	3	6	44	-77	-100	-4	-27	-11	44	173	15	15	-6
Stud's Group, 1972	3	obs.	18	13	12	7	0	11	19	16	8	7	13	21	16
		%dev.	38	15	14	25	-100	-31	2	-6	17	182	-9	25	4
Main Group, 1963-64	20	obs.	30	57	30	7	0	62	137	99	16	28	32	109	100
		%dev.	44	8	24	13	100	8	-6	-9	-6	129	-24	2	25
All censuses combined	96	obs.	127	243	148	50	3	228	317	266	129	138	130	325	277
		%dev.	14	17	-6	-24	90	8	-19	-11	4	154	-17	11	25

Table VI continued

Composition and group ♂♂–♀♀–jj–ii₂–ii₁	No. of censuses		j, i₂	j, i₁	i₂, ♂	i₂, ♀	i₂, j	i₂, i₂	i₂, i₁	i₁, ♂	i₁, ♀	i₁, j	i₁, i₂	i₁, i₁
7-12-9-4-3 (Alto's Group)	3	obs.	0	0	0	4	3	4	1	3	3	1	2	0
		%dev.	100	-100	-100	-5	-2	184	-5	80	-5	-56	90	-100
7-11-7-6-2 (Alto's Group)	3	obs.	7	0	1	9	4	4	0	1	1	2	2	0
		%dev.	78	-100	-72	50	2	19	-100	-15	-50	53	79	-100
7-11-7-5-2 (Alto's Group)	7	obs.	7	0	7	11	7	10	0	2	4	6	2	0
		%dev.	-11	-100	1	-10	11	77	-100	-28	-18	90	-11	-100
7-10-7-4-2 (Alto's Group)	4	obs.	5	0	3	5	6	2	1	2	2	2	1	0
		%dev.	30	-100	-9	-9	55	-9	-100	39	-17	19	4	-100
9-10-7-4-2 (Alto's Group)	2	obs.	5	0	2	4	0	1	1	0	3	1	0	0
		%dev.	178	100	-14	72	-100	-3	96	-100	159	11	-100	-100
7-17-13-2-0 (Main Group)	4	obs.	3	—	0	5	3	0	—	—	—	—	—	—
		%dev.	10	—	-100	49	10	-100	—	—	—	—	—	—
Alto's Group, 1969	5	obs.	9	0	2	11	10	6	0	3	1	2	0	0
		%dev.	14	-100	-67	18	27	28	-100	138	-48	23	-100	-100
Kijiko's Group, 1969	8	obs.	3	0	3	6	4	8	1	0	5	4	2	0
		%dev.	-28	-100	17	-39	-0	117	-48	-100	2	100	9	-100
Spoon's Group, 1969	3	obs.	1	0	3	3	1	3	1	0	1	0	1	0
		%dev.	62	-100	34	-10	-66	46	170	-100	64	-100	170	-100
Tembo Group, 1969	3	obs.	1	0	0	2	2	3	0	1	2	1	0	0
		%dev.	-52	-100	100	-19	-9	233	-100	96	43	-20	-100	-100
Alto's Group, 1971–72	26	obs.	24	0	23	41	26	29	2	10	15	13	9	0
		%dev.	17	-100	-10	0	-10	58	-72	0	-5	16	26	-100
Hook's Group, 1971–72	7	obs.	3	0	5	8	3	1	0	2	7	1	3	0
		%dev.	-28	-100	14	27	-25	-23	-100	-40	45	-67	200	-100
Stud's Group, 1972	3	obs.	4	1	5	5	10	2	0	4	2	1	1	0
		%dev.	-35	-55	-13	-26	62	-19	-100	92	-18	-55	12	-100
Main Group, 1963–64	20	obs.	10	0	4	19	11	5	0	4	12	10	1	0
		%dev.	-20	-100	-39	14	-12	157	-100	-12	4	16	-25	-100
All censuses combined	96	obs.	70	1	55	125	81	70	6	32	55	38	19	0
		%dev.	-24	-98	-17	2	-13	80	-65	14	6	4	14	-100

individuals, so that the cells averaged less than two observations. Second, because a permutation of individuals is comparable to sampling without replacement, the marginal relative frequencies do not provide maximum likelihood estimates for the main diagonal. For example, under the null hypothesis of independence, the probability that a juvenile will be followed by an infant is larger than the probability that another infant will be, since the latter has one less infant (itself) available as a potential infant follower. (Method 7, Appendix, might be appropriate in such a situation.) Finally, if any class had no representative or only one in a census, some cells of the resulting contingency table are known a priori to be zero (cf. Method 8, Appendix).

Our solution, albeit an imperfect one, has been to pool samples from several censuses, then use the usual method for determining expected values from the hypothesis of row-column independence. The last row of Table VI shows the results from all 96 cynocephalus baboon progressions in Sample III combined. The results are highly significant: $P(\chi^2 = 293\cdot5811) \ll 0\cdot001$. In this table, six cells have much larger relative deviations than the others. Five of these are for small infants as followers: they tend to come immediately after adult females, and no others. This is not surprising. Indeed, of the 148 observations in this sample on small infants in the follower position, 123 ($= 83\%$) were infants riding on their mother. The other major deviation was for pairs of large infants, which occurred 80% more frequently than expected. Many of these pairs represent the results of play interactions that persisted even after the group had begun a progression.

We have also carried out some less extensive pooling, in two ways: (1) any censuses, regardless of group, that had the same age-sex composition (though as it happened, no two different groups were ever pooled as a result), and (2) all censuses on the same group in the same study (e.g. five censuses on Alto's Group in 1969, 26 censuses on them in 1971–72). This resulted in 16 pooled samples (two or more progression censuses) in the first case, and eight in the second (total 24), with corresponding increases in sample sizes. Expected cell values and chi-squared values were calculated for each table according to Method 5 (Appendix) if all cells were defined. If some classes were not represented in the group, the corresponding rows and columns were eliminated and the number of degrees of freedom reduced as appropriate.

If some classes were represented by only one individual, so that an a priori zero cell occurred at the corresponding place on the main diagonal, Method 8 was used.

Six of the 16 tables that were pooled from common composition progressions and all eight from single groups were significantly deviant at the 5% level. These 14 deviant pooled samples are given in Table VI. (It is noteworthy that the larger samples were all deviant and that no sample with more than 3·8 observations per cell, on the average, failed to exhibit a significant deviation.) In these 14 samples, too, proximity of infants to their mothers was the major contributor to the deviation. We conclude that Hypothesis 5 is false, primarily because of the mother–infant bond.

6. Adjacency of Adult Males to Others

In watching baboon progressions, one seldom sees adult males adjacent to each other: almost always, individuals of other classes are between them. One gets the impression that the adult males are over-dispersed. Such a possibility is appealing: it could be 'explained', both psychologically, in terms of each male keeping his distance from other adult males, and adaptively, in that none of the other members of the group would ever be far from the protection of an adult male. Of course, it is not surprising that other individuals usually fall between each pair of adult males: because adult males make up a small part of the population, such a pattern is likely to occur often, even if the males are distributed at random through the group. The question is, does this occur more (or less) frequently than one would expect?

> Hypothesis 6. *Adult males are randomly intermixed with members of other classes: the adult males are distributed independently in the positions between the other members of the group and every position is as likely as every other.*

This hypothesis could be tested in several ways. One way is in terms of a classical problem in combinatorial probability theory, in which the males may be thought of as balls that are distributed independently among a set of equiprobable boxes, corresponding to the positions between the other members of the group. A test of the observed distribution can then be based on the number of empty boxes (Method 10, Appendix). Unfortunately, I have not been able to locate an extensive table of this probability

distribution, and the calculations would be very tedious.

A second procedure could be based on the theory of runs (Method 11, Appendix, see also p. 79). A third procedure, and the one that I used, is to take advantage of the fact that the dispersion of the members of a class relative to individuals of other classes invariably affects the frequency with which individuals in a progression are immediately preceded and followed by members of other classes. Suppose, for example, that we classify each individual into one of just two classes, say males and females, and examine pairs of individuals that immediately precede or follow each other in progressions. If males and females are randomly intermixed, the probability of getting a male at any position in the progression, given the sex of the immediately preceding or succeeding individual, depends only on the sex ratio of the remaining uncommitted members of the group. If males and females are not randomly mixed, there are two possibilities: either male–male pairs of adjacent individuals occur more often than expected (males are 'clumped' or 'under-dispersed') or they occur too seldom (males are 'over-dispersed'). In the first case, females too must be clumped, i.e. female–female pairs must in sum be over-represented (and thus male–female pairs and female–male pairs must in sum be under-represented). In the second case, females too must be over-dispersed, i.e. female–female pairs must occur too seldom (and thus male–female and female–male pairs must occur in total more often than expected). Because of these relationships, it is arbitrary whether deviations are analysed and worded in terms of the one class of individuals or the other, though for certain purposes, one approach might be more natural.

The frequencies with which such adjacent pairs are to be expected on the assumption of random mixing can be determined, and these frequencies can be compared with the observed results.

Hypothesis 6a. *In linear progressions, the probability that each individual's nearest preceding and succeeding neighbour is an adult male is independent of the former individual's age and sex, and depends only on the ratio of adult males among the remaining individuals in the group.*

This hypothesis was tested against the two-tailed alternative that adult males were either over-dispersed or under-dispersed in progression orders. We proceeded to test Hypothesis 6a as follows. First, in each progression, we examined every pair of adjacent individuals and tabulated the frequency of each of the four possibilities: an adult male (M) followed by another adult male, an M followed by a non-M, a non-M followed by an M and a non-M followed by a non-M. We then used the hypergeometric probability distribution to calculate the probability, P, of getting exactly the observed distribution. The probability of getting a result at least as extreme as that observed was obtained by adding the probabilities of all possible arrangements of individuals for which the probability is equal to or less than P (see Method 6, Appendix).

Altogether, we have examined 87 progressions in this way (Sample III, Table I, except for one-male groups). Only two had probabilities of 0·05 or less (Table VII). At that fiducial level, about four progressions out of 87 would be expected to show pseudo-significance by chance alone. We conclude that the data are consistent with Hypothesis 6 and Hypothesis 6a.

Perhaps the effect is too subtle to show up in a small sample. In order to pursue this possibility, we have pooled the results of all 87 progressions. The result is 127 male–male pairs, 435 male–other pairs, 437 other–male pairs, and 1836 other–other pairs. Calculation of cumulative hypergeometric probabilities for this set of data would be very time consuming and would not give an exact result, because of end effects in each census; we note that the proportion of

Table VII. Frequency Distributions of Ordered Adjacent Pairs, Adult Males versus Others. The Table Shows the Distribution of the Two Significantly Deviant Samples (5% Level) Out of 87 Available in Sample III. The Probability is the Two-Tailed Hypergeometric Probability of a Result at Least as Extreme as the Observed

Group, date, time	Male–male	Male–other	Other–male	Other–other	Probability
Kijiko, 16 Aug. 69, 0955	2	1	0	15	0·0196
Main, 23 Jul. 64, 1728	2	1	2	30	0·0290

males that followed others (437/2273 = 0·192) is almost identical with the proportion of males in the population (564/2835 = 0·199). We conclude, as before, that the data are consistent with Hypotheses 6 and 6a.

7. Distribution of Adult Males among Adult Females

The lack, in the preceding section, of any demonstrable over- or under-dispersion of adult males relative to individuals of any other class does not preclude the possibility that these remaining classes are not homogeneous, and that the adult males may be over-dispersed in relation to some, under-dispersed in relation to others. In particular, it seems reasonable to ask whether the two adult classes, adult males and adult females, are distributed at random relative to each other, without regard to any intervening immature individuals. We do this by examining the ordering of adult males with adult females, and by taking advantage, as before, of the effect of any non-random ordering on the frequency of adjacent pairs, except that here non-adults will be deleted from the sequence before tabulating adjacencies.

> Hypothesis 7. *In linear progressions, adult males and adult females are distributed at random relative to each other, so that the probability that an adult's nearest preceding and succeeding adult neighbour is a male or is a female is independent of the former individual's sex, and depends only on the sex ratio of the remaining adults in the group.*

We have tested 76 progressions (Sample I, Table I) for randomness of adult males and females (Table VIII), again using Method 6 (Appendix) and testing against the two-tailed alternative of over- or under-dispersion. In only three cases was the cumulative probability, for the two tails combined, equal to or less than 0·05. Thus, the data are quite consistent with Hypothesis 7.

8. Nearest Male Neighbours to Adult Males

If one records the identities of individuals in progression orders, certain pairs of individuals are frequently adjacent to each other. For example, small infants are often immediately in front of or behind their mothers. That particular proximity relationship was so apparent that we shall not pursue it further here. Other relationships were more subtle. At times, we have noticed certain pairs of adult males that were repeatedly each other's nearest adult male neighbour, though without precluding intervening individuals that were not adult males. It seems highly likely that all the adult males of a baboon group recognize each other, and that they have particular preferences in their associations with other males. If so, such 'likes' and 'dislikes' might affect their choice of the adult males to which they are nearest in group progressions.

In order to test this possibility, results from progressions in one group in which the position of every adult male was known (Sample VI, Table I) were tabulated. The frequency with which each adult male was nearest to each other adult male, either preceding or following it, was tabulated in the form of a contingency table with the main diagonal blank (Table IX). Then the value in each cell in the upper right triangle of cells, above the main diagonal, was added to the corresponding cell in the lower left triangle, giving a table of frequencies of nearest male neighbours (Table X). These frequencies range from 0 to 11, suggesting that some pairs of males occur together more frequently than expected, and others less. Of course, in any systematic test of this possibility, it is essential to examine the entire distribution, not just to single out extreme values. We therefore tested the so-called model of quasi-independence, which in this case can be stated as follows:

> Hypothesis 8. *The frequency with which any two adult males are preceding or succeeding nearest*

Table VIII. Frequency Distribution of Ordered Pairs. Adult Males versus Adult Females. The Table Shows the Distribution in the Three Significantly Deviant samples (5% Level) Out of the 76 Cases Available in Sample I. Probabilities as in Table VII

Group, date, time	Male–male	Male–female	Female–male	Female–female	Probability
Alto, 9 Oct. 71, 1823	0	7	6	3	0·011
Alto, 19 Dec. 71, 1140	0	7	7	3	0·0098
Main, 27 Apr. 64, 1419	4	2	3	14	0·045

adult male neighbours is independent of the identity of the males and depends only on the frequency with which each adult male appears in such neighbour relationships.

A formal statement of the quasi-independence model and a method for finding the maximum likelihood estimates of its parameters have been provided by Wagner (1973) and are summarized in the Appendix, Method 9. The method was applied to the data in Table X, using a program written for a Wang 720 computer. (Program available from the author on request.) Values

for the parameters P_i and Q_j were calculated from the marginal totals of Table X. Expected values were obtained from these parameters (cf. Wagner 1969, 1973), and were then compared with the distribution of observed values by means of a chi-squared goodness-of-fit test. The results were not significant at the 0·05 level: $0·75 > P(\chi^2 = 29·27, df = 21) > 0·90$. We conclude that these data do not provide any evidence that adult males show preferences among other adult males as their nearest adult male neighbours in progressions. The comparable problem

Table IX. Frequency of Precedence of Individual Adult Males in 24 Progressions, Sample VI. In Each Column, the Cells give the Frequency With Which the Individual Listed at the Top was the Nearest Following Adult Male of the Individuals Listed at the Left

Male	Next male Ivan	Stubby	Max	Peter	Sinister	Dutch	Cowlick	BJ	Crest
Ivan	–	5	3	2	7	3	4	0	0
Stubby	6	–	6	4	5	3	0	1	1
Max	4	5	–	4	1	5	4	3	0
Peter	1	4	7	–	4	3	1	3	1
Sinister	3	0	1	1	–	6	4	0	0
Dutch	3	3	3	5	3	–	6	2	0
Cowlick	4	1	2	4	2	4	–	0	0
BJ	1	4	1	1	1	1	0	–	1
Crest	0	0	1	0	1	0	1	0	–

Table X. Frequency of Adjacency of Individual Adult Males in 24 Progressions, Sample VI. Formed From Data in Table X by Adding Values in Upper Right Triangle to Corresponding Values in Lower Left

Male	Adjacent male Ivan	Stubby	Max	Peter	Sinister	Dutch	Cowlick	BJ	Crest
Ivan	—	—	—	—	—	—	—	—	—
Stubby	11	—	—	—	—	—	—	—	—
Max	7	11	—	—	—	—	—	—	—
Peter	3	8	11	—	—	—	—	—	—
Sinister	10	5	2	5	—	—	—	—	—
Dutch	6	6	8	8	9	—	—	—	—
Cowlick	8	1	6	5	6	10	—	—	—
BJ	1	5	4	4	1	3	0	—	—
Crest	0	1	1	1	1	0	1	1	—

for adult females will be considered in Section 11.

A reviewer has suggested the use of log-likelihood, presumably meaning the likelihood ratio, rather than Pearson's χ^2 as a test statistic. For incomplete contingency tables, both χ^2 and the likelihood ratio are asymptotically distributed as central χ^2; for small samples, the likelihood ratio has the advantage that it is the statistic that is minimized by maximum likelihood estimates (Bishop et al. 1974). With our samples, no differences in conclusions would result.

9. Precedence Effects in Pairs of Adult Males

Although we have no evidence that adult males exhibit any nearest-neighbour preferences among themselves, it is possible that within each pair there is a tendency for one of them to precede the other whenever they are nearest male neighbour to each other in group progressions. We therefore tested Table IX for independence between the row and column attributes (preceding or following in each pair), again using a model of quasi-independence because of the blank cells.

Hypothesis 9. *The frequency with which each adult male is the nearest adult male ahead of each other adult male is independent of the identity of the males.*

Methods for finding maximum likelihood estimates of the parameters of this independence model have been derived by Wagner (1969, 1973), and are summarized in the Appendix, Method 8. Estimates for the parameters of Table IX were obtained from its row and column totals and are given in the margins of the table. From these, expected cell values were obtained and were then compared with the observed frequencies by means of a chi-squared goodness-of-fit test. The results were not significant at the 0·05 level: $P(\chi^2 = 63·028, \quad df = 55) > 0·05$. Thus the available data provide no evidence that in pairs of adult males, one is more likely to precede, and the other to follow, when they are the nearest adults to each other in progressions. The comparable problem for adult females will be considered in Section 11.

10. Rank-Specific Neighbour Effects in Adult Males

Perhaps the adjacency and precedence effects that were sought in Sections 8 and 9 depend primarily on dominance rank, rather than on the individual. If so, then the failure in the last two sections to find such effects might be attributable

to the fact that the rank order of the males used in compiling Tables IX and X were not constant. We therefore retabulated the same set of data but using dominance rank as the row and column attributes. The results are shown in Tables XI and XII. These two distributions were tested against the status-specific counterparts of Hypotheses 8 and 9, namely:

Hypothesis 10a. *The frequency with which the adult males of any two ranks are nearest adult male neighbours is independent of the ranks and depends only on the frequency with which males of each rank appear in such neighbour relationships.*

Hypothesis 10b. *The frequency with which the adult male of each rank is the nearest preceding adult male to the adult males of each other rank is independent of rank.*

As before, Wagner's procedure was used to obtain maximum likelihood estimates of the parameters P_i and Q_j from the marginal totals of the tables. For Table XI the goodness-of-fit tests gives $\chi^2 = 71·75$, which, with 55 df, is not significant at the 0·05 level. For Table XII, $\chi^2 = 23·88$, which, with 21 df, is not significant at the 0·05 level. Thus, the results are consistent

Table XI. Frequency of Precedence of Adult Males of Each Rank, Sample VI

Rank of male	Rank of next male									Total
	1	2	3	4	5	6	7	8	9	
1	--	5	5	2	1	5	6	1	0	25
2	5	--	2	0	3	5	7	1	1	24
3	5	1	--	5	3	5	3	1	0	23
4	2	6	4	--	5	1	4	0	0	22
5	4	4	3	7	--	3	3	1	0	25
6	1	1	0	2	6	--	2	3	0	15
7	3	2	6	7	4	1	--	1	0	24
8	0	2	2	0	2	1	0	--	1	8
9	1	0	1	1	0	0	0	0	--	3

Table XII. Frequency of Adjacency of Adult Males of Each Rank in 24 Progressions, Sample VI. Data from Table XIII

Rank of male	Rank of adjacent male								
	1	2	3	4	5	6	7	8	9
1	--	--	--	--	--	--	--	--	--
2	10	--	--	--	--	--	--	--	--
3	10	3	--	--	--	--	--	--	--
4	4	6	9	--	--	--	--	--	--
5	5	7	6	12	--	--	--	--	--
6	6	6	5	3	9	--	--	--	--
7	9	9	9	11	7	3	--	--	--
8	1	3	3	0	3	4	1	--	--
9	1	0	1	1	0	0	0	1	--

with Hypotheses 10a and 10b: the data do not provide any evidence for rank-specific preferences among adult males for their nearest adult male neighbours in group progressions, nor is there any evidence that within such pairs the male of one rank or the other is more likely to follow. The comparable problem for adult females will be considered in Section 11, below.

The method of analysis used above considered effects of adult males' ranks only on their nearest adult male neighbours. However, from repeated samples of progression orders, we can tabulate the frequency with which the male of each rank occupies each position among the males, from the first male to the last, and thereby examine the entire distribution at once. This was done for the 24 progressions on one group in Sample VI. The results are shown in Table XIII. A chi-squared test of independence between the row and column attributes gives a highly significant result: $0.005 > P(\chi^2 = 102.02, df = 64)$. The major contributors to this high chi-squared value are scattered through the table and do not form any obvious pattern.

11. Neighbour Effects Among Adult Females

One could formulate four hypotheses that are counterparts, for adult females, to Hypotheses 8, 9, 10a, and 10b. However, in our best available sample (Sample VII, Table I) there were virtually no rank changes among adult females (Hausfater 1975), and it is therefore not possible to distinguish rank-specific effects from idiosyncratic effects. So for adult females, the following two hypotheses were tested:

Hypothesis 11a. *The frequency with which any two adult females are nearest adult female neighbours is independent of the identity (or rank) of the females and depends only on the frequency with which each adult female appears in such neighbour relationships.*
Hypothesis 11b. *The frequency with which each adult female is the nearest adult female ahead of each other adult female is independent of the identity (or rank) of the other females.*

Tables XIV and XV were compiled for adult females, which are listed in rank order, the most dominant at the top and at the left. As with the

Table XIII. Order Among Adult Males of Each Rank in 24 Progressions, Sample VI. The Cells in Each Row Give the Frequency With Which the Males of Each Rank Were Found in Each Position (Front to Back) Relative to Other Adult Males. Below Each Frequency is its Relative Deviation From Observed (Calculated as Observed Minus Expected Value, All Divided by the Expected Value)

Rank of male	1	2	3	4	5	6	7	8	9	Totals
				Position among males						
1	5	5	5	2	3	2	0	1	1	24
	0·5	0·5	0·5	— 0·3	— 0·0	— 0·3	— 1·0	0·2	2·6	2·4
2	6	3	4	7	2	0	2	0	0	24
	0·8	— 0·0	0·2	1·1	— 0·3	— 1·0	0·3	— 1·0	— 1·0	— 1·6
3	1	3	5	6	4	2	2	1	0	24
	— 0·6	— 0·0	0·5	0·8	0·2	— 0·3	— 0·3	0·2	— 1·0	— 0·7
4	2	2	2	2	4	5	7	0	0	24
	— 0·3	— 0·3	— 0·3	— 0·3	0·2	0·5	1·3	— 1·0	— 1·0	— 1·5
5	3	5	1	4	2	7	1	1	0	24
	— 0·0	0·5	— 0·6	0·2	— 0·3	1·1	— 0·6	0·2	— 1·0	— 0·8
6	2	0	1	0	6	5	9	0	1	24
	— 0·3	— 1·0	— 0·6	— 1·0	0·8	0·5	1·9	— 1·0	2·6	1·8
7	2	3	6	2	3	3	1	2	0	22
	— 0·3	— 0·0	0·9	— 0·3	— 0·0	— 0·0	— 0·6	1·6	— 1·0	0·2
8	3	1	0	1	0	0	0	1	0	6
	2·6	0·2	— 1·0	0·2	— 1·0	— 1·0	— 1·0	3·8	— 1·0	1·8
9	0	2	0	0	0	0	0	0	0	2
	— 1·0	6·2	— 1·0	— 1·0	— 1·0	— 1·0	— 1·0	— 1·0	— 1·0	— 1·7
Totals	24	24	24	24	24	24	22	6	2	174
	1·0	5·8	— 1·5	— 0·7	—1·6	— 1·6	— 1·7	2·0	— 1·7	— 0·1

adult males, maximum likelihood parameter estimates for the model of quasi-independence between the row and column attributes were estimated from the marginal totals (Wagner 1973). Neither Table XIV nor Table XV deviated significantly (0·05 level) from the hypothesis of quasi-independence: the chi-square values for these two tables were 80·83 with 89 *df* and 19·87 with 36 *df* respectively. We conclude that the available data provide no evidence that adult females are affected in their choice of progression positions by the identity or rank of their nearest adult female neighbours.

The overall relationship between adult female ranks and position among females was tested by compiling Table XVI, which is in the same format as Table XIII, for males, and is based on the same sample. A chi-square test of independence between the female ranks and positions was significant at the 5% level: $0.25 > P(\chi^2 = 130.47, df = 100)$, but as in the case of the males the most deviant cells formed no obvious pattern.

12. Simulated Progressions

Contrary to my expectations when this study was initiated, the results of this paper suggest that within baboon progressions most of the persistent ordering relationships are subtle

trends, of small magnitude, the major exception being the obvious one of proximity between very young infants and their mothers. Yet during periods of socializing, which often preceded linear progressions, ordered sub-grouping within a group was apparent. Can it be that the mere act of stretching the group out into a line, combined with some individual movement back and forth within the progression, results in an ordering that is difficult to distinguish from a random permutation, particularly if only ordinal and not metric relationships are considered?

There is no doubt that considerable 'shuffling' takes place during progressions. Some individuals walk faster than others, or an individual may pause momentarily, to pick some small morsel of food or pull a thorn from its foot, and will then be passed by several other members of the group. The effects of such shuffling can be seen by comparing two or more censuses taken within a few minutes of each other during a single progression. The orders are virtually never identical, though clearly, too, such progression orders are not independent: the shuffling is far from perfect (cf. Rhine 1975).

In order to test effects of projecting ordered groups onto a line, I carried out some simple simulations. On a large sheet of paper, symbols

Table XIV. Frequency of Precedence of Individual Adult Females, Sample VII. Females are Listed in Rank Order. Female Skinny Disappeared Between the Eleventh and Twelfth Censuses and Thus for Subsequent Samples, the Ranks were Occupied by the Female Listed Immediately Below

Female	Rank	1	2	3	4	5	6	7	8	9	10	11
						Rank of next female						
Skinny	1	–	3	2	3	2	3	3	4	1	3	0
TT	2	2	–	3	2	1	4	3	2	2	3	0
Alto	3	3	1	–	2	1	3	1	3	1	0	2
Mom	4	4	1	2	–	2	5	4	3	1	1	0
Lulu	5	2	4	3	3	–	1	1	4	2	1	0
Fluff	6	3	5	2	0	3	–	2	0	3	4	2
Preg	7	1	2	3	5	3	1	–	0	3	3	0
Scar	8	2	2	3	0	3	4	3	–	1	2	2
Oval	9	3	2	1	3	3	1	1	5	–	4	0
Judy	10	1	2	2	2	1	1	2	1	4	–	4
Ring	11	1	1	1	2	1	0	1	0	2	0	–

Table XV. Frequency of Adjacency of Adult Females of Each Rank in 24 Progressions, Sample VII. Data from Table XIV

Rank of female	Rank of adjacent female										
	1	2	3	4	5	6	7	8	9	10	11
1	–	–	–	–	–	–	–	–	–	–	–
2	5	–	–	–	–	–	–	–	–	–	–
3	5	4	–	–	–	–	–	–	–	–	–
4	7	3	4	–	–	–	–	–	–	–	–
5	4	5	4	5	–	–	–	–	–	–	–
6	6	9	5	5	4	–	–	–	–	–	–
7	4	5	4	9	4	3	–	–	–	–	–
8	6	4	6	3	7	4	3	–	–	–	–
9	4	4	2	4	5	4	4	6	–	–	–
10	4	5	2	3	2	5	5	3	8	–	–
11	1	1	3	2	1	2	1	2	2	4	–

Table XVI. Order Among Adult Females of Each Rank in 24 Progressions, Sample VI. Frequencies and Relative Deviations

Rank of female	Position among females										
	1	2	3	4	5	6	7	8	9	10	11
1	2 / −0·1	1 / −0·5	1 / −0·5	2 / −0·1	2 / −0·1	5 / 1·1	5 / 1·1	3 / 0·3	2 / −0·1	1 / −0·5	0 / −1·0
2	1 / −0·5	0 / −1·0	2 / −0·1	1 / −0·5	3 / 0·3	4 / 0·7	5 / 1·1	3 / 0·3	3 / 0·3	2 / 0·0	0 / −1·0
3	2 / −0·1	1 / −0·5	2 / −0·1	5 / 1·1	1 / −0·5	1 / −0·5	0 / −1·0	3 / 0·3	0 / −1·0	4 / 0·8	5 / 3·7
4	2 / −0·1	5 / 1·1	1 / −0·5	3 / 0·3	3 / 0·3	2 / −0·1	3 / 0·3	2 / −0·1	2 / −0·1	1 / −0·5	0 / −1·0
5	4 / 0·7	2 / −0·1	4 / 0·7	4 / 0·7	0 / −1·0	2 / −0·1	0 / −1·0	1 / −0·5	4 / 0·7	1 / −0·5	2 / 0·8
6	1 / −0·5	2 / −0·1	5 / 1·1	3 / 0·3	5 / 1·1	0 / −1·0	4 / 0·7	2 / −0·1	2 / −0·1	0 / −1·0	0 / −1·0
7	3 / 0·3	2 / −0·1	3 / 0·3	0 / −1·0	2 / −0·1	3 / 0·3	1 / −0·5	5 / 1·1	1 / −0·5	4 / 0·8	0 / −1·0
8	2 / −0·1	4 / 0·7	3 / 0·3	3 / 0·3	3 / 0·3	0 / −1·0	2 / −0·1	1 / −0·5	3 / 0·3	2 / −0·0	1 / −0·0
9	4 / 0·7	3 / 0·3	1 / −0·5	2 / −0·1	2 / −0·1	5 / 1·1	1 / −0·5	3 / 0·3	1 / −0·5	1 / −0·5	1 / −0·0
10	2 / −0·0	3 / 0·3	0 / −1·0	1 / −0·5	1 / −0·5	1 / −0·5	3 / 0·3	1 / −0·5	6 / 1·7	5 / 1·3	0 / −1·0
11	1 / −0·0	1 / −0·0	2 / 0·8	0 / −1·0	2 / 0·8	1 / −0·0	0 / −1·0	0 / −1·0	0 / −1·0	2 / 0·9	2 / 3·1
Totals	24 / −0·0	24 / −0·0	24 / 0·4	24 / −0·5	24 / 0·4	24 / −0·0	24 / −0·5	24 / −0·5	24 / −0·4	23 / 0·5	11 / 1·6

for adult males, adult females, juveniles, small and large infants were arranged in a highly organized (i.e. non-random) way. The composition of this fictitious group was identical with that of one of the groups used in this study (Alto's Group on 8 August 1971), and an attempt was made to arrange the individuals in a way that seemed quite natural for a group of baboons during a social hour: here I put in a juvenile play group, there a cluster of females with their infants, elsewhere a consort pair and even several peripheral adult males (Fig. 3). A direction was then selected at random, and I assumed that each individual simply fell into line according to his or her proximity to the direction of progression (Fig. 3). This gave a simulated progression order, which was analysed in exactly the same manner as was done with the real data. Three analyses were carried out: (1) association between adult males and adjacent others (Method 6), (2) association between adult males and adult females, ignoring intervening immature individuals (Method 6) and (3) independence between age-sex class and progression section (Method 2). This process was repeated five times by choosing a new random direction each time. The resulting probability values are shown in Table XVII. Quite remarkably, only one of these 15 tests was significant at a 0·05 probability level. Thus, even starting with highly organized two-dimensional group structures, the resulting linear projections were

Fig. 3. Simulated group deployment. Composition based on Alto's Group on 8 Aug. 71: seven adult males (♂), 12 adult females (♀), nine juveniles (j), four small infants (i₁), three large infants (i₂).

only occasionally distinguishable from random arrangements. Surely the addition of any 'shuffling' of individuals in these progression orders would only increase the difficulty in detecting what little patterning is evident. Under the circumstances, what is surprising is that we have been able to detect any non-random pattern in the observed progressions.

Discussion
The Adaptive Significance of Progression Orders

Does it matter to baboons whether they walk one behind the other, whether they are near the front or rear of a progression, or whether they are near some individuals and more remote from others? Is it possible that the few weak ordering relationships that do exist in progression orders, other than proximity of mothers and infants, are primarily residual epiphenomena that owe their existence to social interactions established at other times and in other places?

When baboons are foraging in open country, they tend to move in a rank, not a file. Such ranks provide the one other frequently occurring circumstance under which members of a baboon group are arranged in a linear array. The deployment of individuals in such feeding ranks would be worthy of a special study. Elsewhere (Altmann 1974) I have pointed out that a rank is the unique foraging formation that simultaneously minimizes each individual's distance to its nearest neighbour while guaranteeing that each individual will have an exclusive foraging swath. I believe that a reduced rate of food intake for individuals that follow behind numerous others when foraging on sparse, slowly renewing food items is a real and demonstrable phenomenon of a magnitude sufficient to account for the selective advantage of foraging in ranks.

Why, then, do baboons tend to move to and from these foraging areas in a file, instead of a
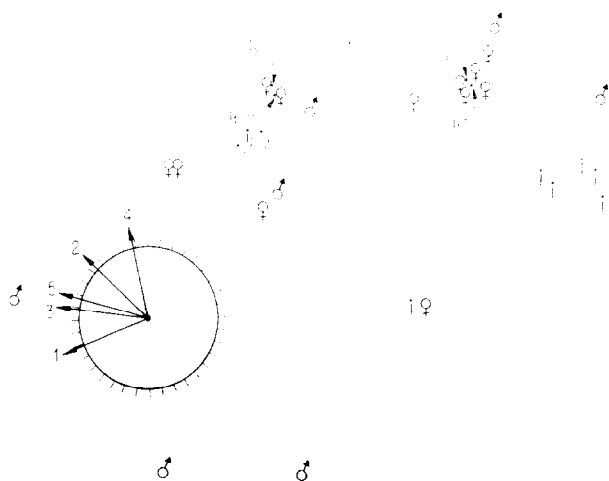
Table XVII. Results of Simulation, Using Fig. 3

Simulation	Probabilities Male-female ordered pairs	Male-other ordered pairs	Age-sex class versus section
1	$P = 1·000$	$P = 1·000$	$0·25 > P > 0·10$
2	$P = 0·6000$	$P = 0·2996$	$0·05 > P > 0·025$
3	$P = 0·3441$	$P = 1·000$	$0·10 > P > 0·05$
4	$P = 1·000$	$P = 0·5781$	$0·10 > P > 0·05$
5	$P = 1·000$	$P = 1·000$	$0·25 > P > 0·10$

rank or even a cluster? I would like to suggest a simple answer: that this is the easiest way to walk when progressing from one place to another. There are several reasons for this. An individual that follows behind another need not search for a route, and in fact gets much information from those ahead, about both major and minor deflections: around this clump of trees, over that log, toward this waterhole rather than that. Conversely, an individual that moves parallel to but considerably to the side of other group members will find that intervening vegetation and terrain make it difficult to maintain visual contact with the rest of the group, which will often be moving along the clearest pathway, and such individuals may stray from the group. These phenomena will be familiar to anyone who has hiked through the woods with a group.

In many areas, baboons appear to take the clearest available routes. It seems reasonable not only that such routes are easier to traverse, but also, in areas with patches of heavy vegetation in which a predator such as a leopard may hide, that such routes may provide the safest available routes, which in extreme form may be compressed into narrow 'passes' (Altmann & Altmann 1970). Beyond that, the route just taken by others may be safer because those that have preceded have not been attacked.

It seems reasonable to hypothesize that the routes taken by baboons during elongated file progressions are sufficiently safe that the possibility of predation ordinarily exerts a negligible effect on the arrangement of individuals within the file, and that appropriate shifts take place only when the group is in a potentially dangerous situation. There are several lines of evidence to support this contention. Members of a baboon group move tensely and compactly when a predator is observed in the area, or when moving through a potentially dangerous area (Altmann & Altmann 1970), but in file progressions, baboons are often spread out over a considerable distance, and the animals usually move in a relaxed manner. Furthermore, individuals often change positions during progressions. A group of playful juveniles may run back and forth. An infant may run to or from its mother. An individual may stop for a few moments to pluck an item of food. Thus, the order of individuals is not invariant even during a single march, but is in a state of flux.

Furthermore, baboons progress in file formation over long distances, through a variety of habitats, and for considerable amounts of time without being attacked. They are not completely immune to attack under those conditions: Glenn Hausfater, Jeanne Altmann and I have all seen attacks on baboons while they were progressing. It is, however, very difficult to obtain data on relative risk rates without long-term studies in which a continuous log of group formation is kept. Probably the most striking pattern found in this study was the tendency for the few deviant progression orders to occur at times when the group was faced with an actually or potentially dangerous situation, not only from predators but from other sources as well (Section 2). In future studies of group geometry, it will be useful to record contextual data for all samples. Special effort should be made to sample groups when they are exposed to danger. Studies of deployment are sometimes difficult at such times, but the necessary data can be obtained, particularly with well habituated groups.

Rhine's Study

During 17 days of August–September 1971, Rhine (1975) carried out a study of progression orders in Amboseli baboons. There are both similarities and differences in our methods, results, and interpretations. Rhine's study was based on a sampling of progression orders in Alto's group, in Amboseli, and that group was one of the most extensively sampled in the present study. Rhine sampled ordinal position across the line of march during all types of group formation. Our samples were taken only during file formations, both because of the greater difficulty in determining order when a group is deployed in other ways and because of the lack of any fixed relationship in such progressions between ordinal position and proximity of individuals. For example, in a dispersed or rank formation, individuals may be separated by considerable distance and by numerous intervening individuals, yet happen to cross the counting line at nearly the same time. This leads to difficulties in interpreting any patterns of ordinal position that may occur. Because our sampling was much more extensive, we could afford to discard records that did not meet fairly strict requirements for accuracy; Rhine included not only complete counts but also those with 'counts in the middle twenties' out of 32–33 individuals, arguing that this minimizes 'bias that might occur as a result of eliminating progressions through bush ... Positions in progressions having a count

different from 32 were transformed proportionately so that the ordinal positions in the data ... ranged from 1 to 32 for all progressions'. No such transformations were used on our data.

Rhine attempted to record as many progression orders as possible, and took samples 'continuously one after another'. As soon as the last animal crossed the counting point, he drove forward along the anticipated line of march for the next count. Rhine refers to each crossing of a point by a group as a separate 'progression', and thus any movement of the group would include an infinity of 'progressions' from which he could sample. We did not follow this procedure, not only because in our experience such a procedure is biased against peripheral trailing individuals but also because such samples are not independent. In fact, Rhine has presented the best available data for this lack of independence: positions are positively correlated in most of his samples that were taken close together, particularly those less than 12 min apart. A similar problem of independence affects many of the analyses in Rhine's paper. Positions of individuals within any one census are not statistically independent, but they are treated as if they were. There are many other differences between Rhine's and my methods of statistical analysis too numerous to detail here.

If one is willing to ignore these differences in methods, several of our results are directly comparable to those reported by Rhine (1975). According to Rhine (1975), adult males tended to be near the front or back, sub-adult males toward the front, and juveniles toward the centre. Dominant males were near the front, subordinates near the rear. In our sample of 97 progressions that were examined for sectional trend, no significant deviation from a random distribution was found in 85 progressions (88 %). Although the remaining 12 cases showed no consistent pattern of deviation, adult males were frequently under-represented in the rear third and over-represented in the front third (cf. Section 2). Our results agree with Rhine's on the tendency of dominant males to be nearer the front than subordinates but the difference was very small: a mere 1 rank difference in mean rank between the front and last thirds of the group. According to Rhine (1975), adult males shift to the front when the group approached a waterhole. In our one deviant sample that was taken at such a time (number 63, Table IV) the seven adult males shifted to the peripheral two-thirds, adult females were over-represented in the rear third, but the two small infants, riding on their mother's ventrum, were in the first and second thirds of the group. The five large infants were all in the central third of the group.

Kinship, Peripheralization and Altruism

The possibility that some individuals voluntarily walk on the periphery of the group and thereby protect the others raises an interesting problem: how could such hazardous, altruistic behaviour evolve? Would not the hypothesized danger on the periphery of the group select against such behaviour? That is, would it not be to the advantage of every individual, regardless of age or sex, to avoid the periphery of the group? The evolution of altruistic behaviour is currently a topic of considerable interest and no attempt to review that topic will be made here. We would like to point out, however, that baboon groups, like those of many other primates, are primarily extended families, with particular stability through the maternal lineage, and are thus well suited to facilitating the evolution of altruism through effects on inclusive fitness (Hamilton 1964); that is, the self-sacrificing altruist may perpetrate his own genotype by increasing the chances that his kin will survive.

Perez Olindo, former Director of Kenya National Parks.

Appendix: Some Methods for Analysing One-Dimensional Group Geometry

'A major problem with spatial patterning as a descriptive concept lies in the difficulty of representing patterns in mathematical terms. Interindividual distances have proven useful in generating quantitative concepts of social distance, group cohesion, group dispersion, etc. To date there is no mathematical procedure for representing other important aspects of social patterning in quantitative terms. Particularly lacking is a model which incorporates age/sex/status variables in defining habitual spatial relationships among members of the group' (Wilson 1972).

Several statistical procedures were followed in testing the hypotheses presented in this paper. The choice of method depended in each case on the nature of the hypothesis being tested. The methods used in this paper and some related methods will be briefly explained below. For convenience, their relationship to particular hypotheses is summarized in Table XVIII.

Criteria of Significant Deviations

For several hypotheses that were tested, it was possible to compute the exact probability of obtaining, as a result of small sample deviations, an outcome at least as extreme as the observed result. By giving probabilities directly, this procedure eliminated the need for statistical significance tests.

Table XVIII. Summary of Methods and Hypotheses

Type of hypothesis	Method of analysis
A. Hypotheses About Invariable Orders	
1. Invariable order. E.g. adult males are invariably at the front and rear of the group	1. Search for counter-examples
B. Hypotheses About Sectional Trends	
2. Section attraction by class. Large group. E.g. adult males tend to be at the front and rear	2. Test for independence in contingency table of section versus class
3. Section attraction by class. Small group	3a. Hypergeometric probability of outcomes as improbable as the observed
	3b. Balls in boxes occupancy probability of outcomes as improbable as the observed
4. Sectional attraction by rank. E.g. low ranking males tend to be peripheral	4. ANOVA or H test of Kruskal & Wallis (1952),
C. Hypotheses About Ordered Pairs (Precedence)	
5. Class attraction and precedence. Large group. E.g. juveniles tend to walk immediately behind an adult female	5. Multinomial distribution. Test for independence in contingency table of class of nth versus $n + 1$st individual
6. Class attraction and precedence. Small group	6. Hypergeometric probability of outcomes as improbable as the observed
7. Class attraction and precedence. Group sizes variable	7. Expected values from model of asymmetric relationships (Altmann & Altmann 1977)
8. Individual attraction and precedence. Repeated samples on a group. E.g. Tom usually follows Bill	8. Test (Wagner 1971) for quasi-independence in contingency table of nth versus $n + 1$st individuals, main diagonal zero
D. Hypotheses about Unordered Pairs (Adjacency)	
9. (a) Individual attraction and adjacency with repeated samples on a group. E.g. Tom and Bill usually are next to each other (b) Class attraction and adjacency in large groups E.g. females are usually next to each other	9. Test (Wagner 1973) for quasi-independence in contingency table of adjacent individuals, upper right triangle zero
10. Class attraction and adjacency. Small group, two classes. E.g. adult males are overdispersed	10. Balls in boxes occupancy probability of at least the observed number of empty slots
11. Ditto.	11. Probability of at least the observed number of runs (Swed & Eisenhart 1943; Barton & David 1957)
12. Ditto.	12. Expected values based on most probable number of runs
13. Class attraction and adjacency. Various sized groups	13. Expected values from model of symmetric relationships (Altmann & Altmann 1977)

There are at least three reasonable interpretations of an outcome that is 'at least as extreme' as the observed result. First, there may be a natural distinction in some situations. For example, in a study of sex ratios in families, either seven or eight boys out of eight children might be considered to be at least as extreme as seven boys. This leads to a one-tailed test. Second, a result 'at least as extreme' might be taken to be one that is at least as far from the mode of the distribution, or alternatively, from each tail. This leads to a two-tailed test. Obtaining seven or eight children of the same sex, whether all boys or all girls, might be regarded to be at least as extreme as seven boys out of eight children. (With a probability of 0·5 that any child will be a boy, and the assumption of Bernoulli trials, the sex ratio distribution is symmetric, and therefore our sex ratio example gives the same results here as in the previous case, but it will not if the probability is different from 0·5.) Finally, 'extreme' may be taken to mean improbable, and thus outcomes at least as extreme as the observed are those whose probability is equal to or less than that of the observed result. Here, too, we are led to a two-tailed test. Throughout this paper 'at least as extreme' is used in this last sense.

Method 1

Any hypothesis that the group has an invariable order, either by individual ('First Tom, then Bill, then ...') or by age-sex class ('Adult and juvenile males in the front, then ...') is quite simple to test: one searches an adequate sample of group orders for counter-examples. If the hypothesis of an invariable order is to be taken literally, then a single counter-example suffices to disprove it.

At this point, we cannot resist setting down a fundamental principle, also known as Altmann's Law, which is as follows: Whatever animals can do, they will do.

From this well-established law, we can derive the following corollary, to be used as a guide to reading the behavioural literature: All statements that tell what animals invariably do, or invariably don't, are invariably wrong.

The only exceptions involve either events so unlikely as to be unrealizable, or violations of the laws of physics or chemistry. That is, animals also obey Altmann's Converse Law: Whatever animals cannot do, they will not do.

Method 2

Suppose the hypothesis is that members of a certain age, sex, rank, or other class tend to be in certain sections or positions in the group (e.g. 'Subordinate adult males tend to be at the front'). Ideally, in testing this hypothesis and others in this paper, we should consider the power of the test rather than the fiducial level. That is, each hypothesis H_0 about non-randomness should be used to generate expected values, and our decision about whether to reject H_0 and accept an alternative hypothesis H_1 of independence between section and class should be based on the probability of rejecting H_0 if it is false.

Unfortunately, the null hypotheses available to us from the literature were too vague to permit calculation of expected values and too unsubstantiated to warrant setting up 'dummy hypotheses' (Hays & Winkler 1971). We therefore tested hypotheses of independence.

Observations were arranged in contingency tables of class versus region or position. Expected values and Pearson's χ^2 were calculated in the usual manner for a test of independence between the row and column attributes. In carrying out such tests we have assumed that the individuals observed in each region are independent replications from infinitely large populations of each class, so that individuals would be multinomially distributed among sections if the attributes were independent. Of course, that is not literally true, and an ideal test would take into account the fact that the number of monkeys in a group is finite (as was done in several methods described below). With large groups, the discrepancy between these two approaches will be negligible. If many results tend to be near the chosen fiducial level, however, consideration should be given to an exact test (cf. Methods 3a and 3b).

Method 3a

Such an exact test could be developed as follows. Suppose that we are concerned with the age-sex distribution of individuals between just two regions, say the centre and the periphery, and that the group contains r_1 individuals of the first kind, r_2 of the second kind, and so forth, with a total of $r_1 + \ldots + r_k = r$ altogether. Then the number of ways of forming from that population a subgroup (say, the peripheral individuals) of exactly n individuals is given by the binomial coefficient $\binom{r}{n}$.

(The notation $\binom{n}{r}$ represents $\dfrac{r!}{n!(r-n)!}$, where

$x! = x(x-1)(x-2)\ldots 1$.

By convention $\binom{r}{n} = 0$ if $r > n$, and $0! = 1$.)

Of all those ways, the number of them that will result in a subgroup with n_1 individuals of the first kind, n_2 of the second kind, and so forth $(n_1 + \ldots + n_k = n)$ is given by

$$\binom{r_1}{n_1} \cdot \ldots \cdot \binom{r_k}{n_k} .$$

Therefore, on the assumption that all combinations of individuals that meet these specifications are equally likely, the probability of the observed distribution is given by

$$p(n_1, \ldots, n_k) = \binom{r_1}{n_1} \cdot \ldots \cdot \binom{r_k}{n_k} \div \binom{r}{n} ,$$

which is the multivariate form of the hypergeometric probability distribution.

From the hypergeometric distribution, one can readily develop formulae for calculating the probabilities of special cases that may be of interest, e.g. the probability that a subgroup of size n contains only individuals of one specified kind, the probability that members of just one specified class are not included, and so forth. In each case one could then add to this the probability of all distributions more extreme (less probable), but without an algorithm for finding all such distributions, the computation problemwould be enormous except for very small (sub)groups.

Method 3b

If just one class of individuals, say adult males, has been singled out, then a somewhat different null hypothesis would lead to other procedures. Suppose that we define sections of the progression order (e.g. front, middle, rear) in terms of positions between those individuals that are not adult males. For example, suppose that a group includes eight individuals that are not adult males. Then adult males in front of the first non-male, between the first and second, or between the second and third could be regarded as being in the front section, those between the third and fourth, between the fourth and fifth, or between the fifth and sixth could be regarded as being in the middle section, and the rest of the males could be regarded as being in the rear section. We now have a 'balls-in-boxes' problem, described in Method

4, except that in this case, the number of 'balls' (adult males) is so large compared with the number of 'boxes' (sections) that few boxes would ever be empty, thus ruling out the procedure of Method 4. Alternatively, one could calculate, for each progression, the probability of the observed occupancy distribution, then add to this the probability of all more extreme distributions. These procedures make no assumptions about group size, but the calculations would would be very laborious unless an algorithm can be obtained for finding all distributions with smaller probabilities (cf. Method 10).

Method 4

Suppose that the members of a group or class can be rank-ordered in some way (e.g. by dominance status, by age, etc.) and we would like to know whether there is any relationship between ranks of individuals and the section of the group (e.g. front, centre, rear) in which they occur. We may be willing to assume that the distributions of ranks in the sections have essentially the same shape and differ only in their mean. The usual procedure for testing such a hypothesis about differences in means is the analysis of variance with a single criterion of classification, using a chi-square test when the variance of the parent population is known and an F test when it is not. This topic is discussed in basic statistics books. That method is applicable not only to rank orders but to other characteristics, including measurements that do not have ordinal and integral values. Analysis-of-variance tests for comparison of means assume approximate normality in the distributions of characteristics within each sample (section) although they are reasonably robust against non-normality (Box & Anderson 1955). Analysis of variance also assumes independence of sampling, to which rank-ordered individuals do not conform. For example, knowing the total number of adult males in a group and the mean ranks of males in the front and centre sections of a progression, the mean rank of those in the rear third could be calculated.

An alternative procedure, which we have used for testing the results of unpooled progression samples, is the H test of Kruskal & Wallis (1952, 1953). That method makes no assumption of normality and is particularly suitable for rank-ordered data. The test statistic to be computed is

$$H = \frac{12}{N(N+1)} \sum_{i=1}^{c} \frac{R_i^2}{n_i} - 3(N+1)$$

where

c = the number of regions;
n_i = the number of observations (individuals) in the ith region;
$N = \Sigma n_i$, the number of observations in all regions combined;
R_i = the sum of the ranks in the ith region.

Large values of H lead to rejection of the null hypothesis that there are no differences in ranks between regions. Appropriate tables are given by Kruskal & Wallis (1952, 1953), for three regions ('samples' in their terminology) and for n_1, n_2, $n_3 \leqslant 5$.

The next several techniques (Methods 5–10) are concerned with hypotheses about dispersions or 'attractions' of members of one class to individuals of other classes, rather than to specific regions or positions.

Method 5, but group size or class size is quite small, so that we cannot ignore end effects and the effects of sampling without replacement, the procedure of Method 5 is inapplicable. We now describe an exact test that is appropriate in such circumstances.

Suppose, for simplicity, that we divide the population into just two classes of individuals, say males (M) and females (F), and examine all pairs of adjacent individuals. We can tabulate the frequency of the four possible combinations: M → M, M → F, F → M, F → F. Let us designate these four frequencies by n_{11}, n_{12}, n_{21}, and n_{22}, respectively. The frequencies can be arranged in the form of a contingency table (below), in which the row represents the class of the individual at each position y in the line, and the column represents the class of the individual immediately behind it.

		Next individual		
		Male	Female	Totals
	Male	n_{11}	n_{12}	$n_{11} + n_{12}$
yth *individual*	Female	n_{21}	n_{22}	$n_{21} + n_{22}$
	Totals	$n_{11} + n_{21}$	$n_{12} + n_{22}$	$N = n_{11} + n_{12} + n_{21} + n_{22}$

Method 5

Suppose that our hypothesis is about a tendency of individuals of certain classes to walk immediately in front of, or immediately behind members of certain other classes (e.g. infants that are not riding on their mother tend to walk immediately behind an adult female) and we want to look at the entire distribution of adjacent pairs. Data on adjacent leader-follower pairs in progressions can be tabulated in the form of a contingency table (e.g. Table IX), with the row representing the class of the lead individual of each pair and the column representing the class of the individual immediately behind it. If there are k classes of individuals, then the contingency table will have k rows and k columns. If we are analysing a sample obtained from a single large group, then under the null hypothesis of independence in the attributes of adjacent individuals, the observations will have an approximately multinomial distribution, and the usual chi-square test of independence between row and column attributes can be used (Method 2).

Method 6

If we are testing an hypothesis about the ordering relationships between classes, as in

The marginal totals of this table either will be the numbers of individuals in the two classes, or will differ by one from the true values as a result of end effects, whenever the first and last individuals are in the same class.

There are

$$\frac{N!}{(n_{11} + n_{21})! (N - n_{11} - n_{21})!} = \binom{N}{n_{11} + n_{21}}$$

ways, all assumed by hypothesis to be equally likely, for arranging the $n_{11} + n_{21}$ males and the $N - n_{11} - n_{21}$ females in a linear progression

order. Of this total, there are $\binom{n_{11} + n_{12}}{n_{11}}$

arrangements of the $n_{11} + n_{12}$ males; for each

of these, there are $\binom{n_{21} + n_{22}}{n_{21}}$ ways to arrange

the remaining $n_{21} + n_{22}$ females. Hence the probability of getting exactly the observed

distribution is obtained from the hypergeometric probability distribution:

$$p = \frac{\binom{n_{11} + n_{12}}{n_{11}} \binom{n_{21} + n_{22}}{n_{21}}}{\binom{N}{n_{11} + n_{21}}}$$

The hypergeometric probability distribution is described in almost all general texts on probability or statistics (e.g. Feller 1957; Mosteller et al. 1961: Brownlee 1965). The probability of getting a result at least as extreme as that observed is obtained by adding the probabilities of all possible arrangements of individuals for which the probability is equal to or less than p.

This procedure can be illustrated by a graph (Fig. 4). It was constructed as follows. The data from one sample (number 2, Table VIII) were tabulated in the form of a two-by-two contingency table:

is at variance with our hypothesis of independence. The computations for our tests were carried out on a Wang 720 computer for which a special program was written by S. S. Wagner and V. Jones, to whom I am most grateful.

Those familiar with Fisher's exact test for a two-by-two contingency table will recognize that our procedure is a two-tailed version of Fisher's test, which is one-tailed; that is, Fisher's test utilizes only outcomes that deviate from the mode in the same direction as the observed.

An alternative method for obtaining the two-tailed hypergeometric probabilities has been described by Lieberman & Owen (1961), namely, take double the one-tailed cumulative probabilities, which can be obtained from their *Tables of the Hypergeometric Probability Distribution*. For purposes of comparison with our exact method, our program also computes this approximation. We advise against their method. Comparisons with the results of exact probabilities calculated by means of our program

		Next adult		
		Adult male	Adult female	Total
	Adult male	0	7	7
*y*th *adult*	Adult female	7	3	10
	Total	7	10	17

The hypergeometric probability distribution (Method 6) was then used to calculate the probability of this outcome, seven male–female pairs (upper right cell of table) given the marginal distribution and the hypothesis of independence. (Any other cell could have been used.) The result is $p = 0.0062$. We then examined all other two-by-two tables with these same marginals. There are eight altogether, corresponding to upper right cell frequencies from zero to seven. For each such table, we calculated the probability of getting exactly that outcome, and plotted these figures on the graph. We now ask, what is the likelihood of obtaining a result at least as extreme as the observed result? The answer can be obtained by adding all probabilities in Fig. 4 that are at least as improbable as that of the observed distribution. The appropriate values are shown by open circles in Fig. 4. Their sum is $P = 0.0098$, which is less than 0.05. That is, the observed distribution of pairs deviates significantly at that level and therefore

indicate that for a number of our tables there is a considerable inaccuracy in results obtained by the approximation. This inaccuracy results from
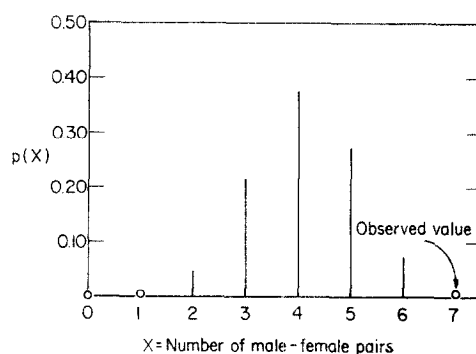

Fig. 4. Hypergeometric probability distribution for sample of 19 Dec. 71 (Table VIII). The three open circles indicate outcomes at least as improbable as the observed. Their total probability is 0.0098, indicating a significant deviation of the observed outcome from the hypergeometric model.

the asymmetry of the hypergeometric probability distribution.

The hypergeometric probability test has been described above for two classes of individuals but can readily be extended to a multivariate form (Feller 1957). Unfortunately, the amount of computation rapidly becomes unmanageable. Some suggestions for computations in the three-class case have been presented by Leyton (1968).

Method 7

Suppose that we have an hypothesis about ordered pairs (e.g. dyad precedence) and that we have pooled the results of several samples taken on the same group at times of different compositions, or even various groups with different compositions (e.g. Table VI). A method for obtaining expected values from the null hypothesis of independence between the class of the first and second members of each pair has been derived (Altmann & Altmann 1977). Let t_y denote the number of samples on groups with the yth population composition and let m_{xy} and m_{zy} denote the number of individuals in class x and class z respectively during each of those samples. Then for all samples combined, the expected number $E_{x, z}$ of ordered pairs x, z can be estimated from

$$
E_{x, z} = \begin{cases} \sum_j \dfrac{N t_j m_{xj} m_{zj}}{\displaystyle\sum_{i,j} t_j m_{ij}(\sum_k m_{kj} - 1)} & \text{if } x \neq z; \\[20pt] \sum_j \dfrac{N t_j m_{xj}(m_{zj} - 1)}{\displaystyle\sum_{i,j} t_j m_{ij}(\sum_k m_{kj} - 1)} & \text{if } x = z. \end{cases}
$$

We assume that the usual χ^2 test for contingency tables can be applied to the deviations between these expected values and the observed values.

Method 8

Suppose that frequencies of leader-follower pairs in many progressions of a group are cross-tabulated by individual, rather than by age-sex class (e.g. Table IX). Then the cells along the main diagonal of the table will be blank or undefined because an individual cannot follow himself. (In the literature, such cells are sometimes referred to as being 'a priori zero'. It is important that such a priori zeros not be confused with observed values of zero, such as may occur in any of the other cells of the table.) In such contingency tables with a blank main diagonal, how does one test the hypothesis of

independence between the row and column attributes? That hypothesis is equivalent to the hypothesis that for every pair of individuals i, j there exist non-negative parameters P_i and Q_j with $\Sigma P_i = \Sigma Q_j = 1$ such that $p_{ij} = P_i Q_j / \Sigma P_i Q_j$ for all $i \neq j$, and $p_{ij} = 0$ for $i = j$ (Wagner 1969). The P_i's may be regarded as the tendency of the ith individual to be the lead member of the pair, and the Q_j's may be regarded as the tendency of the jth individual to follow. The problem now becomes that of finding the values of the parameters P_i and Q_j that maximize the likelihood function. A method for doing so has been provided by Wagner (1969); see also Method 9, below.

Methods 5-8 above deal with ordered pairs of individuals. Methods 9-13 deal with unordered pairs, such as individuals that are adjacent to each other but for whom the order within the pair is not considered.

Method 9

Suppose we are analysing the frequency with which individuals are adjacent to each other regardless of the order within pairs. Then the observed frequencies of adjacencies can be tabulated in the form of a contingency table in which the main diagonal and the upper right triangle are blank. For example, Table X was obtained from Table IX by adding the frequency in every cell i, j in the upper right triangle of the latter table to the frequency in the corresponding cell j, i in the lower left triangle of the table. Similarly, if samples of adjacent pair classes (not individuals) are drawn from a large population, so that sampling without replacement produces a negligible effect on probabilities, the results can be tabulated in the form of a contingency table, but in which only the upper right triangle, not the main diagonal, will be blank.

If our null hypothesis is that position in progressions is independent of the identity (or class) of adjacent individuals, we have a problem involving quasi-independence, similar to that of Method 8, but with a different configuration of blank cells. Wagner (1973) has provided a general solution for such incomplete contingency tables, regardless of the configuration of blank cells. He has found the necessary and sufficient conditions for the likelihood function to have a maximum, and has provided an iterative procedure for finding the maximum likelihood estimates of the parameters P_i and Q_j. With the assistance of V. Jones, he has written a program for a Wang 720B computer equipped with

output printer. That program was used for the analysis of all incomplete contingency tables in this paper that were being tested for quasi-independence. A copy of the program is available from S. S. Wagner or the author.

Method 10

Suppose that we are interested in the dispersion of members of some one class through the group. For example, we hypothesize that adult males are over-dispersed relative to other individuals. Such questions are equivalent to a classical problem in combinatorial probability. To pursue the problem in terms of the dispersion of adult males, we regard the positions between the non-males as slots or boxes, and the males as balls. We assume as our null hypothesis that the balls are distributed independently among these slots and that the probabilities of a ball falling into each slot are the same. If there are f non-males in the group, there are $f + 1$ slots between them, including the positions before the first and after the last non-male. Under the null hypothesis, what is the probability that at least y of these $f + 1$ slots will be empty, i.e. what is the probability of observing y or more pairs of adjacent non-males (including any first or last non-male as forming an adjacent pair)? Equivalently, we can take one minus the probability of observing at most $x = y - 1$ occupied slots. The probability of having x or less cells occupied when N balls are randomly and independently distributed among k equally probable cells is given by

$$H(x,k,N) = \sum_{i=1}^{x} \binom{k}{i} \sum_{j=0}^{i} (-1)^j \binom{i}{j} \left(\frac{i-j}{k}\right)^N$$

where

y = the observed number of 'empty slots' (pairs of adjacent individuals of the second class, including any first or last non-males);

$x = y - 1$;

k = the total number of slots $= f + 1$, where f is the number of individuals in the second class;

N = the number of individuals of the first class.

If the members of the first class (adult males, in our example) are over-dispersed, the number of empty cells (adjacent non-males) will be too small. Conversely, if they are over-dispersed, the number of empty cells will be too large. A table of critical points of this distribution is given in

Owen (1962, Table 17.2), but for values of k that are too small for our purposes.

Because of the possibility that the summation from $i = 1$ to $i = x$ will include not only the tail of the distribution but the mode and much of the rest of the distribution as well, it might be preferable to calculate the probability of obtaining exactly the observed frequency of empty slots, then add to this the probability of any frequency that is less likely (Method 3). Such a procedure would be in accord with our policy in this paper of regarding outcomes 'more extreme' than the observed to be those that are less likely. Unfortunately, I have not been able to locate a table of this distribution, and the calculations would be quite tedious.

Note: I recently learned that a small unpublished table of these point probabilities has been prepared by Nicholson (1960; cited in Nicholson 1961) for $K = N = 3$ (1) 20, and is available from that author on request. According to Nicholson (1961), David (1950) has suggested other tests for groups larger than those for which Nicholson provides a cumulative probability table (reprinted in abbreviated form in Owen, 1962, as Table 17.2). Other, potentially more sensitive combinatorial procedures would take into account the distribution of the number of balls per slot, not just the number of occupied slots (Feller 1957, Chapter II), and in general, several parts of the theory of occupancy may be applicable to analytic studies of group geometry (Barton & David 1968, and references therein). Two alternative approaches will be considered below (Methods 11 and 12). These methods are compared on p. 79.

Method 11

Another way to test for randomness of dispersion of the members of one class, say males, among the others is as follows. Suppose that males are over-dispersed, i.e. that they tend to be more spread out in progression orders than they would be if they were randomly and independently distributed among non-males. If so, then 'runs' of non-males will occur in the progressions more frequently than expected. (A 'run' is an unbroken sequence of items of the same kind, in this case non-males.) Conversely, if males are under-dispersed ('clumped'), then runs of non-males will, on the average, be longer and there will be fewer of them. Thus, the hypothesis of a random distribution can be tested by considering the distribution of runs. Let m be the number of individuals in one class

(e.g. males) and let f be the number in the other class (females). Then if all distinguishable arrangements of males and females are equally likely, the probability of having exactly k runs of females is, according to Feller (1957 : 60),

$$\binom{f-1}{k-1}\binom{m+1}{k}\binom{m+f}{f}$$

The chance of getting at least k runs of females is therefore

$$\sum_{i=k}^{f}\binom{f-1}{i-1}\binom{m+1}{i}\binom{m+f}{f}$$

(The summation stops at f because there can be no more than f runs of females.) Alternatively, we could find the cumulative probability of all arrangements of m individuals of one class and f of the other for which the probability was equal to or less than the probability of the observed arrangement.

Statistical tests based on the theory of runs have been worked out by Swed & Eisenhart (1943) for the bivariate case and by Barton & David (1957) for the multivariate case. Brownlee (1965) discusses approximations that can be used for values that exceed those tabulated by Swed & Eisenhart.

Method 12

If the group is not large and we are only concerned with adjacency (unordered pairs) for two exclusive and exhaustive classes of individuals, say males and females, the problem can be looked at as that of finding the probabilities or expected values for the three classes of unordered pairs, M–M, M–F, and F–F, given the assumption that the members of each class may be treated as indistinguishable (i.e. do not result in different ordering) and that all distinguishable orderings of M's and F's are equiprobable.

In this case, the most probable number of 'runs' (strings of all M's or all F's) is one of the three or two integers k such that

$$\frac{2mf}{m+f} < k < \frac{2mf}{m+f} + 3,$$

where m and f denote the number of males and females, respectively (Feller 1957: 60, no. 21). We note that the number j of M–F pairs must be one less than the number of runs:

$$j = k - 1.$$

Now imagine that each monkey in the line holds hands with the one ahead of him and the one behind. Let us account for the $2m$ male hands and the $2f$ females hands. With the most probable number of M–F pairs there are j male hands and j female hands committed to M–F pairs. (1) If j is odd, then there must be a male at one end of the line and a female at the other. The remaining $2m - j - 1$ male hands will form $(2m - j - 1)/2$ M–M pairs. Likewise, there will be $(2f - j - 1)/2$ F–F pairs. (2) If j is even, the end members must be of the same kind (sex). The chance that a given end will be a male should equal the proportion of uncommitted hands that are male; thus the expected value for the two ends should be twice that:

$$\frac{2(2m-j)}{2m+2f-2j} = \frac{2m-j}{m+f-j}.$$

The expected number of M–M pairs will be half the number of male hands not committed to M–F pairs or to ends:

$$E(M\text{–}M) = \frac{2m - j - \dfrac{2m-j}{m+f-j}}{2}$$

and similarly for females

$$E(F\text{–}F) = \frac{2f - j - \dfrac{2f-j}{m+f-j}}{2}$$

The remaining pairs must all be M–F.

Now, we note that there will be three or two values of k (and thus of j) that are most probable. Each of these values leads on to an expected value for each type of pair. We can take the mean of these as the final expected value. The observations can be arranged in the form of a 3×1 contingency table (M–M, M–F, F–F) and tested against these expected values.

Method 13

When analysing adjacency in pooled samples from several progressions, either on the same or different groups, we may encounter a situation in which we are combining results from progressions involving different numbers of individuals in each class. This problem was treated in Method 7, which dealt with the analysis of independence in ordered pairs. Here we consider the comparable problem for unordered pairs. An appropriate method for obtaining expected values for the

frequencies of adjacencies has been derived by Altmann & Altmann (1977). Let m_{xy} and m_{zy} be the number of individuals in the xth and zth class respectively in each sample with the yth composition, and let t_y be the number of progressions sampled with the yth composition. Then for any unordered pair of classes xz the expected number E_{xz} of adjacent pairs of type xz is given by

$$
E_{xz} = \begin{cases}
\dfrac{N \sum\limits_{j} t_j m_{xj} m_{zj}}{\sum\limits_{\substack{i,k \\ i<k}} \sum\limits_{j} t_j m_{ij} m_{kj} + \frac{1}{2}\sum\limits_{i}\sum\limits_{j} t_j m_{ij}(m_{ij}-1)} & \text{for} \\[4pt]
\quad \text{each unlike-class pair } (x \neq z); \\[10pt]
\dfrac{\frac{1}{2}N \sum\limits_{j} t_j m_{xj}(m_{xj}-1)}{\sum\limits_{\substack{i,k \\ i<k}} \sum\limits_{j} t_j m_{ij} m_{kj} + \frac{1}{2}\sum\limits_{i}\sum\limits_{j} t_j m_{ij}(m_{ij}-1)} & \text{for} \\[4pt]
\quad \text{each same-class pair } (x = z)
\end{cases}
$$

where N is the total number of observed pairings in all sample groups combined. We assume that the usual χ^2 test for contingency tables can be applied to the deviations between observed and expected values, if allowance is made for the degrees of freedom that are lost from the blank cells.

Comparison of Small-Sample Methods

It would be interesting to know more about the types of over-dispersion and under-dispersion to which the small-sample methods (Methods 3, 6, 7, 10–13) are sensitive, but such an analysis is beyond the scope of this study. Ostensibly, they are asking different questions, some about occupancy, say by males of slots between females (Methods 3 and 10), some about numbers of runs of individuals of the same class (Methods 11 and 12), and some about adjacent pairs (Methods 6, 7 and 13). However, we note that the components of these three approaches, namely number of unoccupied cells, number of runs, and number of each type of adjacent pair, are intimately related: for two classes of individuals, say male and female, (1) the number of runs must be one greater than the number of male–female adjacencies, and (2) the number of unoccupied slots between females is the same as the number of female–female adjacencies plus one for each 'terminal' female (first individual or

last). Thus, the three tests are probably sensitive to essentially the same kinds of dispersion patterns and it seems likely that essentially the same results will be obtained with each. Second, we note that none of these methods is sensitive to one particular type of dispersion: differences in the mean numbers of intervening individuals of the opposite kind. This can readily be seen in the following illustration. Let us write 0 for a male and | for a female. Now consider the following two progression orders: (1) 0|0|0||||||||, and (2) 0|||0|||0|||. Both have the same number of unoccupied slots between females (seven, including the space to the right of the right-hand female), the same number of runs (six), and the same number of pairs of each kind: M→M, M→F, F→M, F→F (namely 0, 3, 2 and 6, respectively). Yet surely there is some sense in which the males in the second progression are more widely dispersed than those in the first. Perhaps a more satisfactory test in this case could be based on the size distribution of runs of females that intervene between males.

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