

The Order of Movement of Yellow Baboons (*Papio cynocephalus*)

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Abstract. The spatial organization of progressing baboons is thought to serve a protective function considered important in their adaptation to a terrestrial existence. Progression positions of identified black infants, adult males, and other yellow baboons were determined from repeated samples of troop movements. Spatial positioning by demographic class was similar to that previously found for three troops of anubis baboons living in two different habitats. Such consistency across species and habitats seems unlikely unless it arises from a common genetic background or common ontogenetic stabilizing mechanisms.

Introduction

The use of space within and between groups is an important aspect of social organization among primates and other vertebrates [e. g., CARPENTER, 1964; COLLIAS, 1944; ELLEFSON, 1968; HALL, 1966; MARLER, 1968; MASON, 1969; SOMMER, 1969; WILSON, 1972; WYNNE-EDWARDS, 1962]. Conspecific spacing appears in the complex equation of primate evolution because of its impact upon the regulation of fundamental biological processes, such as aggression and mating, and its role in the regulation of conditions of species survival, such as use of vital resources and protection of the group. In this paper, attention is focused upon the protective function of the spatial organization of moving troops of baboons.

In early studies by WASHBURN, DeVORE and HALL [DEVORE, 1964; DEVORE and WASHBURN, 1963; HALL and DEVORE, 1965; WASHBURN and DEVORE, 1961a, b], spatial organization within progressions of moving baboons was

thought to serve a protective function of considerable importance for the understanding of primate evolution:

'The actual variability of progression order of baboons when on the move deserves careful study, particularly in view of DEVORE and WASHBURN's interesting suggestion that the formation assumed by a moving group of baboons is of great significance in the baboons' adaptations to a terrestrial mode of life.' [ALTMANN and ALTMANN, 1970, p. 188].

During movement, dominant adult males and vulnerable young were reported in the troop's center, while subordinate and subadult males tended to be near the troop's front or rear. It was reasoned that this spatial formation would protect vulnerable animals by placing two tiers of powerful males between them and potential danger. It was also noted, when an actual danger source was seen, that changes in troop positioning of the adult males tended to leave them between the troop and danger. For example, DEVORE and WASHBURN [1963, p. 344] report the following incidents:

'On one occasion we saw two dogs run up behind a troop, barking. The females and juveniles hurried ahead, but the males continued walking slowly. After a moment an irregular group of some twenty adult males was between the dogs and the rest of the troop. When a male turned on the dogs, they ran off. On another day we saw three cheetahs approach a troop of baboons. A single adult male stepped toward the cheetahs, gave a loud, defiant bark, and displayed his canine teeth; the cheetahs trotted away.'

In the presence of more formidable danger sources, such as lions or humans, the entire troop may flee, and this fleeing may be highly adaptive, as when baboons climb into trees to escape lions but come down from trees to escape humans.

Studies of anubis (*Papio anubis*), yellow (*P. cynocephalus*) and chacma (*P. ursinus*) baboons at several locations indicate considerable variation in spatial arrangements during progressions. WASHBURN and DEVORE [1961a, p. 95] noted that the central positioning of dominant males and vulnerable young 'is clearest when the troop is moving rapidly and may vary considerably when the troop is moving slowly, feeding as it goes'. Variation in movements patterns also occurs when a subgroup of 'adult and older juvenile (subadult) males and adult females sometimes move rapidly ahead to a new feeding spot' [DEVORE and WASHBURN, 1963, p. 342], leaving the rest of the troop behind. Both ROWELL [1969] and HARDING [1973] found adult males near the front or back of progressions. Some vulnerable young tended to be centrally located, but there was no evidence of any such tendency for mothers carrying infants. On the other hand, RHINE and OWENS [1972] found that mothers

carrying black infants tended to enter a potentially dangerous clearing after other adults arrived and to leave while other group members still remained; although these data were not obtained from full progressions, they suggest that mothers with black infants probably occupied a somewhat central position in movement through the area. Neither ALTMANN and ALTMANN [1970] nor STOLTZ and SAAYMAN [1970] detected systematic progression orders in their study troops, although STOLTZ and SAAYMAN [1970] and SAAYMAN [1971] did note that certain males tended to be in front of the troop more often than other animals and ALTMANN [1973] suggests the existence of subtle ordering principles.

Given the evidence of variability, it is instructive to restate some of WASHBURN and DEVORE's main themes without reference to specific spatial positioning of different demographic groups. The protection theory of spatial organization assumes a nonrandom arrangement by age-sex category. As a consequence of this nonrandom protective arrangement, the probability of exposure of the more vulnerable troop members to a foreign danger is assumed to be less than the corresponding probability for the more self-sufficient members. If the large, aggressive adult males are the primary source of protection, signs of boldness and confidence should be manifested in their behavior, and conversely, if adult males are bolder than other group members, then some other members should manifest more signs of fearfulness and caution than adult males.

The positioning of vulnerable young and dominant males in the troop's center is only one of several possible formations which are consistent with a protection theory of spatial organization. The mode of predator attacks on baboons and the effect of progression position on mortality are still undetermined. Central positioning of dominant males and vulnerable young may be an optimal protective formation under conditions where the probability of attack is equal from all directions, but it may not be optimal if the probability of attack is greater from some directions than from others. For example, if the troop is heading into a clump of bush, fearful young might tend to bring up the rear, whereas these animals might be near the front if the troop is moving out of bush into open country. Similarly, older experienced animals might tend toward a particular position in the troop formation under some circumstances and toward different or random positioning under other conditions. The actual formation of most progressions would not necessarily depend upon the immediate direction of danger, which the troop may not even perceive, but rather upon some combination of experience and behavioral genetics determined by predation and other selection pressures. Experience

teaches adults and possibly others the general types of situations from which danger is likely to arise, and the specific situations where danger was previously met. For example, WASHBURN and HAMBURG [1965] report an incident in which a baboon troop shot at just once thereafter remained wary of men, and ALTMANN and ALTMANN [1970] found complete avoidance of a commonly used sleeping site after two troop members had been killed there by a leopard. Similarly, as numerous cases of habituation to observers demonstrate, baboons also rapidly learn about safe conditions.

In a species as intelligent as the baboon, almost any form of social behavior, spatial or otherwise, could understandably exhibit considerable variation arising from the baboon's ability to adapt to features of his world. Indeed, besides variation in progression order due to possible boldness, fearfulness, and specific experiences, one might also expect variation associated with factors such as speed of the troop's movement, troop density, terrain, vegetation, local tradition of the particular troop, and immediate sensing of frightening or safe conditions.

Accurate detection of spatial arrangements associated with these different conditions depends upon sampling and observation techniques. STOLTZ and SAAYMAN [1970] looking at a troop as a whole were unable to detect a systematic spatial arrangement, whereas HARDING's [1973] and ROWELL's [1969] repeated observations of the order of movement yielded quantitative data which displayed a more orderly picture. ROWELL's and HARDING's progression data were obtained from census counts for which sampling probably occurred when observation conditions were particularly good and when the mode of troop movement made accurate censusing possible. Thus, ROWELL selected twenty good, 'more or less single file' progressions, and left out progressions by 'disorganized drift'. This sampling procedure is appropriate in a study focusing primarily upon population dynamics, but for the present study, where progressions are the center of interest, a more representative sampling procedure is desirable. From the point of view of data bearing upon a theory of protective order, a disorganized drift is just as interesting as a neat file: If a specific spatial order has functional importance why is it manifested in some progressions and not others, if indeed it is?

In order to approximate a representative sample of progressions, it is necessary to recognize when a progression is occurring and to decide when in its progress a record of the spatial arrangement should be made. The troop does not always move in unequivocal starts and stops, progressing without pause to a new location and then coming to a complete halt again. Instead, it may move somewhat erratically, but more or less continuously, for most

of the day, and even when the troop appears to be doing nothing more than feeding and meandering, it may be making slow progress in a direction consistent with the larger pattern characterizing the day's overall movement throughout the range. Progressions may be defined in relation to an entire day's movement, from leaving the sleeping trees or cliffs in the morning until they are entered again at dusk. For this study, *a progression is defined as the order of movement of the troop across any point on the day's total line of march*; consequently, in an ordinary day, there is an infinite number of possible progressions from which a sample can be taken. A representative sample would include many progressions taken throughout the troop's range, and selected without eliminating in advance any kind of progression moving through any particular kind of situation.

In the research reported here an attempt was made to record as many progressions of yellow baboons per day as possible. Data from these progressions will be compared with previous findings and related to the theory of protective organization.

Method

Location and Troop

Observations of progression order were made on a troop of yellow baboons being studied by ALTMANN and ALTMANN and their associates in the Masai-Amboseli Game Reserve, Kenya. The ecology of Amboseli baboons has been described in detail [ALTMANN and ALTMANN, 1970], and their habitat has been summarized by STRUHSACKER [1967, p. 892] as follows:

'The Masai-Amboseli Game Reserve lies in the plains immediately to the north of Mount Kilimanjaro and is located 2°40'S, 37°10'E, with an elevation of about 3,700 feet... Temperatures range from 48 to 90°F, sometimes within a 24-hour period. The annual precipitation of 10 to 20 inches is restricted to 2 periods; November through December and March through May. The habitat at Amboseli is typified as semi-arid savanna, having a small number of plant species. Permanent water holes and swamps within the Reserve are fed by springs arising from the underground drainage of Mount Kilimanjaro. Near these permanent sources of water there are relatively dense groves of fever trees (*Acacia xanthophloea*) with an understory dominated by *Azima tetra-cantha* and *Salvadora persica* shrubs. Living in these groves were greater concentrations of vervet monkeys than I observed anywhere else in East Africa. Other primates in the Reserve were baboons (*Papio cynocephalus*), bush babies (*Galago senegalensis*), and Masai tribesmen. Furthermore, there were at least 18 species of ungulates, 15 species of carnivores, and a wide

variety of birds. All animals within the Reserve were protected against hunting. The only source of human disturbance to the Reserve was overgrazing by the domestic stock of the Masai people.'

By 1971, when the progression research was conducted, the dense groves of fever trees and other vegetation had been greatly thinned [STRUHSAKER, 1973; WESTERN and SINDIYO, 1972].

During the period of nearly all of the observations, the study troop contained 32 animals. Using the age-sex categories of ALTMANN and ALTMANN [1970, p.21], the troop contained 7 adult males, 11 adult females, 2 juvenile-2 males, 5 juvenile-1s, 5 infant-2s, and 2 black infant-1s. Individuals recognized and identified during recordings of progression order were as follows: all adult males (*Stubby* [SB], *Peter* [P], *Ivan* [I], *Dutch* [DT], *Sinister* [SN], *Cowlick* [C], and *Max* [M], both black infants and their mothers (*Mom* and her infant *Kub* [K] and *Preg* and her infant *Dogo* [D]), both juvenile-2 males (*Ben* [B] and *Even* [E]), and three juvenile-1 males (*Stiff* [SF], *Red* [RD] and *Russ* [RS]). HAUSFATER's [personal commun.] records indicated at the time of the study that the three most dominant adult males were *Stubby*, *Peter*, and *Ivan* (probably in that order), the next in line were *Dutch*, *Sinister*, and *Cowlick* (probably in that order), and the last was *Max*, who was the smallest and probably the youngest. Possibly *Max* would have been categorized as size 5 or subadult in ROWELL's [1969] classification. The larger of the juvenile-2 males (*Ben*) was approximately size 4 to 5 in Rowell's scheme and the smaller approximately size 4.

The probable effect of predation was seen in the disappearance of four troop members shortly before the study began [HAUSFATER, personal commun.], the disappearance of a mother and her infant and of a juvenile near the beginning of the study, and the loss to lions of an adult female and her son shortly after the study was completed [HAUSFATER, personal commun.].

Procedure

Progression order was recorded sitting atop a field vehicle which had a hatch in the roof. An attempt was made to anticipate the direction of movement and then to drive the vehicle approximately 20 m ahead of the troop and park it so that the observer's line of sight to a stationary object, such as a tree, made a 90-degree intersection with the line of march. As the animals crossed the observer's line-of-sight their names were called into a tape-recorder if they were identified; if not, they were called simply as *other*. On a few occasions when the troop was very spread out along the line of sight, some animals passed the counting point behind the vehicle. In these cases, the line of sight was extended behind the vehicle and the

progression was recorded if the animals were separated enough and passed slowly enough to allow a count by looking back and forth from front to rear; otherwise, the progression had to be cancelled. Occasionally one or more animals (usually playing juveniles) passed the counting point and then reversed direction and recrossed it. Such an animal was subtracted from the count and recounted when it passed again, in which case his order in the progression was the position occupied on the last crossing. If there was enough fast back-and-forth movement to confuse the count, the progression was cancelled.

An attempt was made to record as many progressions (orders of movement across counting points) as possible during 17 of the days of August and September, 1971. Progressions were recorded continuously one after another, except for a few early in the study taken as the opportunity arose. As soon as the last animal crossed the counting point, the observer drove forward along the line of march and parked in advance of the troop for the next count; consequently, many of the progressions recorded were sequential samples of a continuous flow of movement. In driving forward and parking, care was taken to avoid herding the animals or to park in a position that would influence their movements. The troop was being observed simultaneously from a second field vehicle, and on a few occasions the two vehicles happened to stop in a position where the troop had to walk between them. If the vehicles were too close together, some troop members seemed to hurry their progress. Similarly, some animals hurried if they passed quite near a single vehicle, especially if they were somewhat separated from other troop members.

A total of 194 progressions was recorded as completely as possible. As indicated in table I, most counts totaled to 32, which was the actual troop size except for 14 early progressions when the troop had 33 members. Table I suggests that counting errors were most commonly errors of omission; however, counts of less than 32 were not necessarily in error since some animals, especially adult males, were sometimes known to be temporarily separated from the troop at the time of the progression. Counts in the middle twenties all occurred in bush heavy enough to obscure the passage of some animals but light enough to allow observation of the order of those animals who were seen. These counts were retained to reduce bias that might occur as a result of eliminating progressions through bush. Even so, many such progressions either could not be recorded in the first place or had to be cancelled. As a consequence of counts less than 32 and of identification errors (e.g., the same animal called twice in a progression), the number of progressions in which the order of an identified baboon was known varied from animal to animal. Observations of the smaller juvenile-2 and the three juvenile-1 males began after several progressions were recorded; the resulting number of progressions for these four animals ranged from 98 for *Even* to 167 for *Russ*.

Cancellation of progression recordings occurred when it became evident that the order of movement could not be correctly determined. In addition to cancellations due to obscuring bush, other cancellations occurred when the line of march was incorrectly anticipated or changed in the middle of a count, when animals split into subgroups involving substantial numbers of animals which did not cross the counting point, when an alarm sent many animals scurrying back across the counting point, when the movement pattern appeared to be unduly influenced by a research or other vehicle, and when several animals moved too rapidly across the counting point to be individually noted and recorded.

In addition to the order of movement across a counting point, several other items of data were collected, as follows:

Time of progression: The elapsed time from the first to the last animal passing the counting point, timed to the nearest half minute at both the start and end of the progression.

Table I. Number of animals recorded in counts of 194 progressions

	Number of animals recorded											
	24	25	26	27	28	29	30	31	32	33	34	
Number of progressions	1	2	3	0	5	10	23	45	92	12	1	

Vegetation: The density of vegetation through which the troop was progressing. Vegetation was recorded as *open* (an area with little bush, trees, or high grass as in figure 1A), *bush* (an area of considerable trees, bush, or grass where a predator could readily hide, as in figure 1B and the background of figure 1C), and *open-bush* (a progression through an open area fringed with considerable vegetation, as in figure 1C).

Formation: The general shape in space of the progressing troop. The formation was categorized as *file* (elliptical shape, with the long axis being the line of march), *flank* (short axis of an ellipse in the line of march), *file-flank* (a mixture of file and flank, either simultaneously or during different parts of the progression), and *neat file* (an elongated ellipse in more or less single file, with only a few animals abreast, as in figure 1D).

Action: The type of movement best characterizing the progression. Action was categorized as *running*, *mixed walking and running*, *walking*, or *meandering and feeding*.

Distance between initial and final centers of mass: The estimated distance between the center of the troop's mass when the first animal arrived at the counting point to its center of mass when the last animal passed the counting point. A gross approximation of the whole troop's *speed of movement* during progressions is the distance between the centers of mass divided by the time of the progression.

Results

The main data are the ordinal positions in which identified animals passed the counting point in each progression. Black infants usually crossed the counting point riding ventrally on their mothers. One black infant (*Kub*) crossed 11 times by itself and once carried by an adult male, and the other black infant (*Dogo*) crossed by itself only once. Since a riding black infant and its mount crossed simultaneously, they were assigned the mean of the two ordinal positions they occupied. Thus, if a mother with a riding infant crossed after the sixth animal, both infant and mother were assigned positions 7.5 and the next animal in the progression was ninth. Positions in progressions having a count different from 32 were proportionately transformed so that ordinal positions in the data presented below ranged from 1 to 32 for all progressions.

Systematic Ordering

If individual animals tend to occupy the same position in independent progressions, there should be a positive correlation among ordinal positions occupied by identified animals in randomly selected pairs of progressions. Twenty pairs of progressions were randomly selected, with each member of the pair subject to the following conditions: (1) each progression in the pair must have occurred on a different day; (2) one of the pair had to occur before 12:00 h and the other after, and (3) if one of the pair occurred during 11:00 to 12:00, then the other could not have occurred from 12:00 to 13:00. The twenty correlations ranged from -0.64 to 0.60 with a median of 0.19 . There were 15 positive and 5 negative correlations, a difference significant at the 0.05 level by the sign test. Even with selection procedures designed to minimize dependencies among pairs of progressions, there appears to remain a slight tendency for individual animals selectively to occupy similar ordinal positions from one progression to another.

This slight tendency toward systematic positioning may be compared with positioning in pairs of successively occurring progressions. Correlations were calculated on all pairs of successive progressions for which the start time of the second was 10 min or less from the end time of the first. There were 114 such correlations having a median of 0.42 and ranging from -0.75 to 0.92 . The median correlation of 0.19 from the 20 random progressions is significantly different from the median of 0.42 from the 114 successive progressions ($\chi^2 = 13.22$, $p < 0.001$), indicating in addition to the slight tendency to take the same position in independent progressions a tendency to keep the same position for at least 10 min; of course, a correlation of only 0.42 leaves ample room for considerable switching of positions.

Ten successive progressions further illustrate the tendency for consistency from one progression to the next, as well as the gradual interchanging of progression positions among different animals. These 10 progressions were recorded following an alarm which sent the troop scurrying in neat file for a considerable distance through open country. By repeatedly counting and driving ahead, it was possible to sample this march ten times during approximately 45 min of continuous movement. Figure 2 is a plot of all possible pairs of the ten progressions. The numbers on the abscissa of figure 2 indicate the separation in the pairs of progressions entering into the correlations plotted above them. Thus, the nine points plotted above '1' are all pairs of successive correlations (first and second, second and third, third and fourth, etc.); the eight points above '2' are all pairs of progressions twice removed from each other (first and third, second and fourth, third and fifth, etc.) and

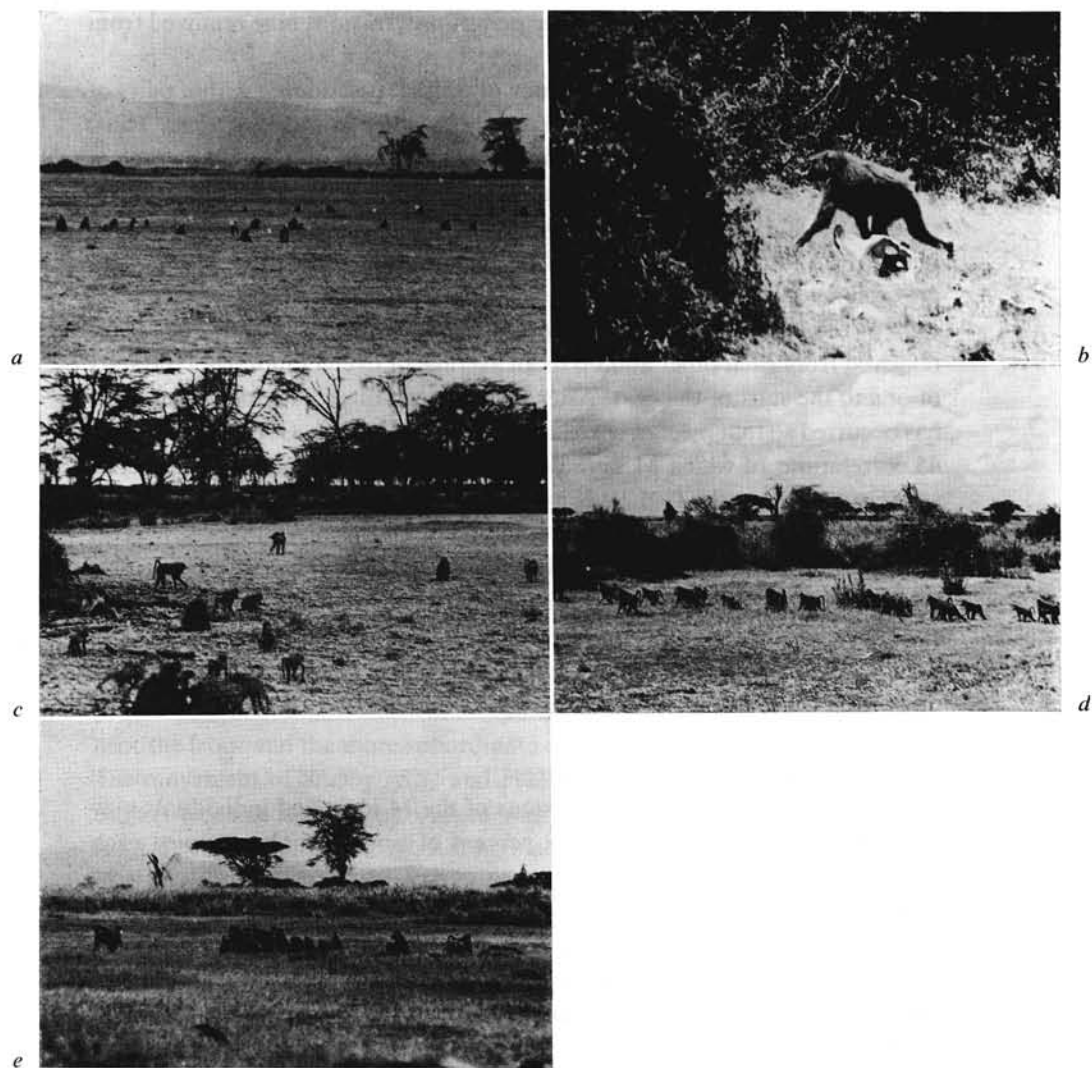


Fig. 1. Examples of three vegetation categories (A = open, B = bush, and C = open-bush), a neat-file progression (D), and a compacted spatial arrangement (E).

so on to the single correlation for the pair of progressions nine removed from each other (first and tenth).

There was considerable consistency of ordinal positioning within pairs of progressions not too far removed from each other in order or time. Thus, the nine pairs of successive correlations have a median of 0.77 and a range of 0.43–0.92. The mean recorded time from the start of one of these progressions to the start of the next in the pair was 4.4 min, and the range was 2–10 min. (Mean times from the start of one to the start of the other paired progression are given at the top of figure 2 for each set of correlations.) Consistency in the order of movement appears to hold through progressions three removed from each other and up to an average of over 12 min from the start of one to the start of the next. After that, enough interchanging of positions has occurred so that median correlations are close to zero. Overall, there were 45 correlations of which 34 were positive and 11 were negative, a difference significant beyond the 0.01 level by the sign test. Up to and including progressions three removed from each other, 22 of the 24 correlations were positive ($p < 0.01$), whereas only 12 of the remaining 21 were positive ($p > 0.25$). Perhaps this series of neat file progressions approximates the maximum expected consistency; slower, more relaxed progressions, with feeding and socializing, probably offer many more opportunities for interchanging positions from the recording of one progression to the next.

Positioning of Demographic Classes

Patterns in the progression positions of the 14 identified individuals may be seen from curves indicating the percent of time animals occupied each of the 32 positions. In constructing such curves, progression positions were expressed in integers, and progression positions of black infants were rounded down, creating a slight frontward bias. For graphs of progressions, the 14 identified animals were divided into demographic classes as follows: six adult males of which three were more dominant (*SB, P, I*) and three more subordinate (*DT, SN, C*), three subadult males (*M, B, E*), three juvenile males (*SF, RD, RS*), and two black infants (*K, DG*). *Subadult males* covers a broad transitional period between the three juvenile-1 males and the older adult males. This period was the best available approximation to HARDING's [1973] subadult category with which comparisons will be made below.

Figure 3 shows individual curves by demographic class for all progressions in which the individuals were identified. Two aspects of these curves stand out. First, the pattern of progression positions appears to differ by demographic class. Adult males tended to be near the front or back of progressions, with

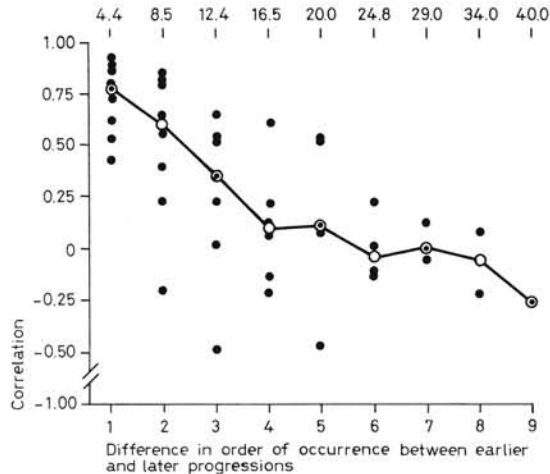


Fig. 2. Correlations among identified individuals as a function of the closeness of progressions. Open circles are median correlations, and solid dots are individual correlations. On the abscissa, 1 refers to pairs of progressions once removed (first and second, second and third, etc.), 2 to pairs twice removed (first and third, second and fourth, etc.), and so on. Numbers at the top of the figure are the average times from the start of the first progression in a pair to the start of the second.

the two most dominant males in this particular troop being by far most often near the front and the more subordinate ones being most often near the rear. The movement of *Stubby* (*SB*) and *Peter* (*P*) so often near the front is due in part to cases where they walked well ahead of the rest of the troop for several progressions in a row. Riding black infants appear to be spread more or less equally across progression positions, except perhaps for the front and rear blocks, though these blocks are by no means empty. Subadult males tended to be near the front quarter of the progressions and were infrequently found in the rear. The juvenile males also were found infrequently near the rear, but unlike the subadults they were more often near the center of the troop than the front.

A second notable aspect of the curves is the degree of consistency among individuals within classes. Except possibly for the curves of *Ivan* (*I*) and *Sinister* (*SN*), there is considerable similarity among individual curves within a demographic class, and even the curves of *Ivan* and *Sinister* are more like those of adult males than those of other demographic classes. It is tempting to consider *Ivan* as transitional between the patterns of the dominant and subordinate males; however, a certain amount of variation from the main pattern is hardly surprising among animals as intelligent as baboons.

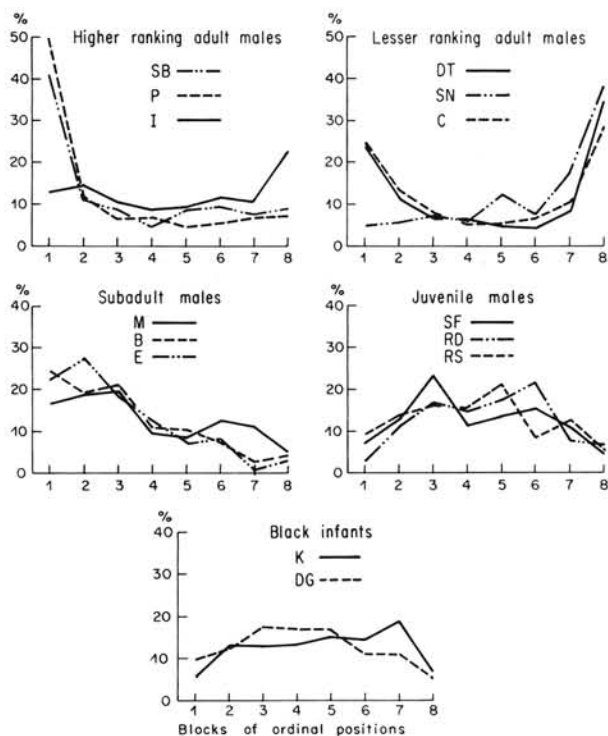


Fig. 3. Percentage of progressions in which individual animals were counted in each of 8 successive blocks of 32 ordinal positions. Front is 1 and rear is 8.

Figure 3 is based upon all 194 progressions; as indicated by the correlations reported above, positioning in some of these progressions was correlated with positioning in subsequent progressions. To examine positioning by demographic class with this relationship minimized, a set of progressions was selected according to the following criteria: (1) one progression was randomly selected each day from among those starting and ending at 12:00 h or before; (2) another progression was similarly selected from among those occurring after 12:00, and (3) the start time of an afternoon progression from a given day was at least 1 h later than the end time of the morning progression from the same day. These criteria yielded 29 progressions having an average time of 4.80 h from the end of the first to the start of the second of those progressions occurring on the same day (range of 2.43–8.62 h).

Figure 4 is a comparison of curves of progression orders yielded by the 29 randomly selected progressions and the curves from all 194 progressions.

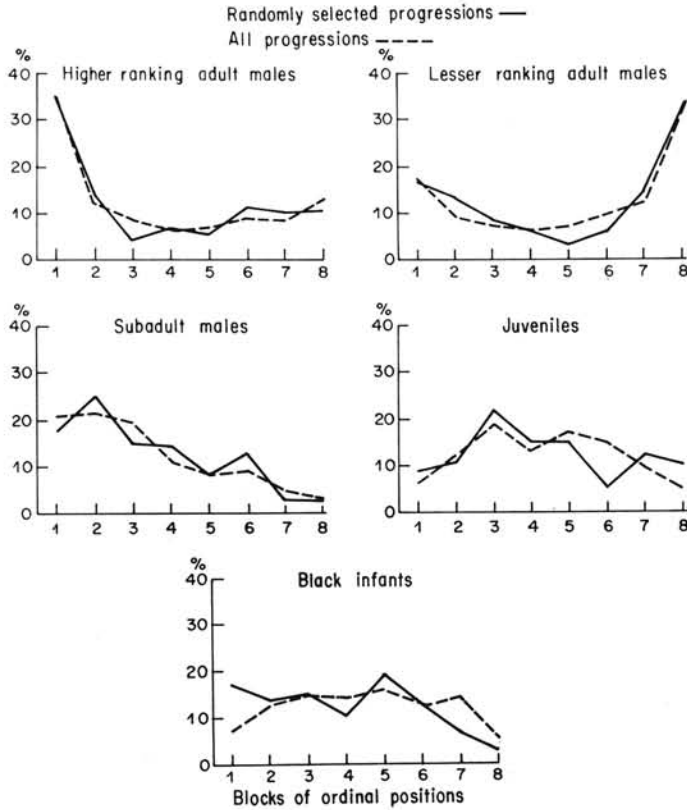


Fig.4. Percentage of randomly selected progressions and of all progressions in which animals were counted in each of 8 successive blocks of 32 ordinal positions. Front is 1 and rear is 8.

Progression order by demographic class is similar for both kinds of curves. It is also similar for the broad trends of the 14 individual curves underlying the overall curves, except that the individual curves from the 29 progressions were less regular than the corresponding curves from 194 progressions, as would be expected from the difference in sample size.

Figure 5 depicts progression order as a function of the type of formation the progression assumed. Progression patterns do not differ in any distinct way as a function of formation. The curves for flank progressions are perhaps more irregular than the others, probably due to the occurrence of only 18 progressions taking that shape. It was thought that fast moving, neat file pro-

gressions might have a somewhat different pattern than other types. The present data from 40 such progressions indicate that neat file progressions follow approximately the same pattern as the other formations. When the neat file progressions were plotted for individual adult males, the resulting curves closely paralleled those of figure 3.

The 194 progressions were also divided into those occurring in different vegetation types (open, bush, and open-bush), and once again the resulting curves for each demographic class followed the same general trends appearing in figures 3-5. Overall, these trends became smoother as n increased and persisted regardless of the selection criteria adopted.

Comparative Analysis

Progressions of Amboseli baboons were compared to anubis baboons by transforming data from the Amboseli study and two others into a comparable form. One of the comparison troops was studied by HARDING [1973] near Gilgil, Kenya, and data from two further comparison troops appeared in ROWELL'S [1969] study of baboons living near Ishasha camp in Queen Elizabeth National Park, Uganda. The Gilgil troop ranged through grassland, with few trees, and slept in cliffs; the Ishasha troops occupied riverine forest bordered by grassland, which the baboons did not use extensively. Predator pressure appeared to be greater upon the Amboseli troop than upon the Gilgil or Ishasha troops; large carnivores were seen more frequently at Ishasha than at Gilgil, where the study troop ranged through a cattle ranch. At Ishasha, S-troop contained approximately 30 members and V-troop approximately 60. The Gilgil troop had approximately 50 members. Thus, an Amboseli-Gilgil-Ishasha comparison involves two species, three studies, and four troops of varying sizes living in quite different habitats.

Progression data from the four troops were transformed proportionately so that all progressions were divided into 6 blocks of ordinal positions instead of 8 (Amboseli), 5 (Gilgil), and 12 (Ishasha-V). Data for Ishasha-S were published in a graph already containing 6 blocks of progression positions. The 12 blocks in the graph of Ishasha-V were readily reduced to 6 by combining adjacent pairs of blocks. Gilgil data were presented numerically as the percent of time the members of a demographic class were counted in each block of progressions, with the total for all blocks within a demographic class being 100%. Ishasha data were plotted by a method yielding totals within demographic classes different from 100%; therefore, the value for each plotted block of Ishasha progressions was read from its graph and transformed proportionately so that the data from each of the three studies could be plotted

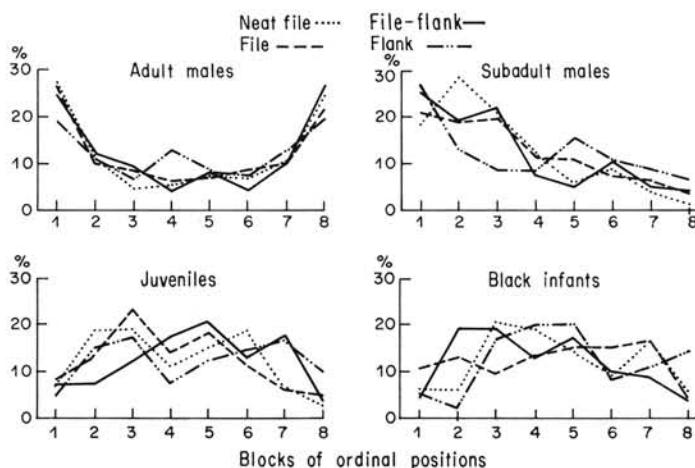


Fig. 5. Percentage of progressions for each of four formations in which animals were counted in eight successive blocks of 32 ordinal positions. Front is 1 and rear is 8.

for six blocks of progression positions per demographic class, with the values for each set of blocks adding to 100%.

Data from Amboseli and Ishasha were available for four demographic classes, while the Gilgil data were divided into nine classes. Data were available in all three studies for adult males, and in the Amboseli and Gilgil studies for black infants. The Gilgil data contained a class for subadult males and a next younger class of large juveniles of both sexes. The Amboseli class of subadult males was established to approximate the corresponding Gilgil class. Ages of Amboseli juveniles were equivalent to Ishasha small juveniles, which in turn were approximately equivalent to Gilgil small and median juveniles. Gilgil and Ishasha juvenile classes contained both sexes, whereas identified Amboseli small juveniles were males only. Insofar as progression order is concerned, differences among sexes are probably more important for large juveniles and older animals than for smaller juveniles. The data for approximately equivalent demographic classes are indicated by the curves in figure 6.

A two-factor analysis of variance was performed on the values plotted in figure 6, with the four demographic classes as an independent factor and the six blocks of progression positions as a repeated-measures factor. The apparent difference among the four sets of curves is confirmed by a highly significant interaction between demographic classes and progression positions ($F = 14.62$, d.f. = 15, 45, $p < 0.001$). In addition, highly significant differences among the

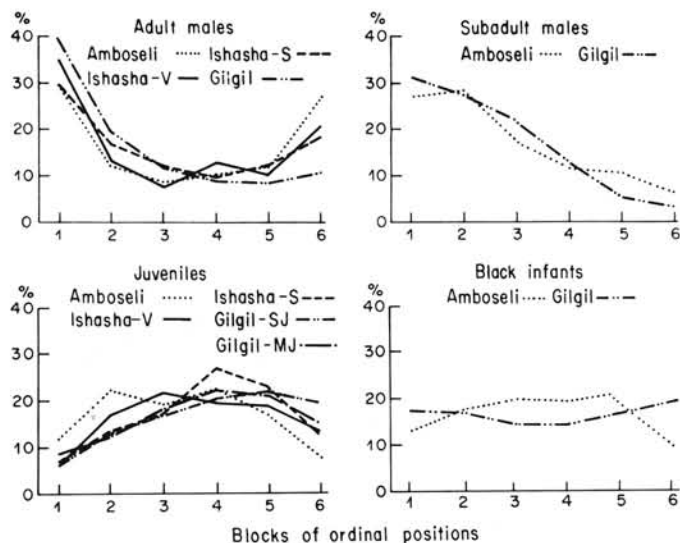


Fig. 6. Comparison of progression orders by demographic class and by study areas. In 6 blocks of successive ordinal positions, 1 is front and 6 is rear.

six blocks of positions occurred for adult males ($F=23.85$, d.f. = 5, 45, $p<0.001$), subadult males ($F=15.33$, d.f. = 5, 45, $p<0.001$), and juveniles ($F=9.10$, d.f. = 5, 45, $p<0.001$), but not for black infants ($F=0.34$).

Figure 6 depicts a remarkable degree of consistency among curves based upon different species, different habitats, different troops, and different study techniques. The occurrence of such consistent patterns seems unlikely in the face of so many opportunities for variation unless these patterns arise from a common genetic background or common ontogenetic stabilizing mechanisms. If that is the case, it would be expected that other troops of yellow and anubis baboons, and chacma and possibly Guinea baboons, would also be characterized by similar spatial patterns. Satisfactory quantitative evidence to check this hypothesis is not yet available.

Table II compares by demographic class the observed and expected percent of animals in the first and last progression positions. Expected values for juveniles of the Ishasha troops were estimated using the number of adult males most commonly seen in each of the troops to make proportionate estimates from published curves of juvenile positioning. This method yields estimates for V-troop of 11 adult males and 21 juveniles in a total of approxi-

Table II. Percent of progressions in which members of various demographic classes of four troops were in the first or last positions

Position	A♂	p ¹	SA♂	p	Juv	p	BI	p
Observed first								
Amboseli	64.6	0.001	8.6	ns	0.0	0.001	0.5	0.001
Gilgil	50.0	0.001	4.0	ns	1.3	0.001	0.0	0.01
Ishasha-S	46.0	0.01			5.0	0.01		
Ishasha-V	56.0	0.001			0.0	0.001		
Observed last								
Amboseli	55.7	0.001	0.7	0.001	1.4	0.001	0.5	0.001
Gilgil	23.7	0.001	0.0	ns	21.1	ns	5.3	ns
Ishasha-S	31.0	ns			16.0	ns		
Ishasha-V	55.0	0.001			10.0	0.02		
Expected first (last)								
Amboseli	18.8		9.4		9.4		6.3	
Gilgil	7.7		2.6		27.1		8.9	
Ishasha-S	16.7				30.0			
Ishasha-V	18.3				35.0			

¹ Numerical entries in columns headed 'p' are significance levels from a binomial comparison of expected and observed frequencies. Nonsignificant probabilities (ns) are all greater than 0.10.

mately 60 troop members, and a similar estimate for S-troop of 5 adult males and 9 juveniles in a troop of approximately 30.

Table II indicates that adult males either led progressions or brought up the rear far more often than expected by chance. Subadult males were first just about as often as expected, but they were rarely last. Juveniles and riding black infants were first far less often than expected by chance. They were last less often than expected in the Amboseli troop and in one of the two Ishasha troops; neither juveniles nor black infants of the Gilgil troop were last less often than expected. Avoidance of the rear position by juveniles and by mothers carrying black infants parallels probable differences in predator pressure, which appeared to be greatest at Amboseli and least at Gilgil. However, on several occasions, Amboseli mother-infant pairs were seen last during progressions in which they were subsequently recorded elsewhere. On such occasions, mothers looked up from feeding, resting, or walking, and saw the main body of the troop moving forward. Then, the mothers began moving briskly or accelerated a slower pace so that they passed the counting point before less agitated troop members. This behavior suggests that mothers car-

rying infants may have a more nervous disposition than other adults and it deserves systematic study using measures more appropriate than the order of movement.

At Amboseli, the more dominant adult males were first in 41.4% of the progressions and last in 8.8%. A reversed trend occurred for the more subordinate adult males which were first in 23.2% of the progressions and last in 46.9%. The frequencies underlying these figures were analyzed by a chi-square for a four-fold contingency table. A highly significant result ($\chi^2 = 286.67$, $p < 0.001$) indicates that the more dominant adult males tended to be first and the subordinate adult males tended to bring up the rear. This pattern may be only a peculiarity of the particular age-sex, social, or other features of the Amboseli troop or habitat since the five adult males studied by HARDING [1973] all tended to be more toward the front than the rear and only one was ever counted last. The positioning of dominant and subordinate males is particularly interesting in any consideration of troop protection; further comparative data are needed to investigate habitat, population and social variables as possible causes for frontward or rearward tendencies among differently situated troops.

Progressions into Water Holes

Where there is permanent water, there is likely to be cover for predators. WASHBURN and DEVORE [1961b] noted that baboons approached waterholes with great care. Similarly, ALTMANN and ALTMANN [1970] described cautious behavior in a troop's style of drinking, with only a few animals drinking at a time and others looking about. Alarms and predator attacks occurred disproportionately often near waterholes, especially during the dry season when rain pools away from cover were unavailable.

In the present study, progressions into waterholes tended to be more cautious than most other progressions, though on a few occasions the animals seemed to approach a waterhole with little or no hesitancy. Animals heading progressions frequently slowed down or stopped in front of a waterhole, allowing the rest of the troop gradually to catch up and causing it to become compacted just before moving in to drink. Often when the troop stopped in front of a waterhole, some animals climbed trees and others looked toward the water. An adult usually (possibly always) was the first to walk toward the water; after a few adults had moved forward, others from the compacted troop followed in file behind them. Once the first several had drunk, the animals appeared more relaxed, and after drinking they usually foraged and socialized near the edge of the waterhole or a short distance away. On several

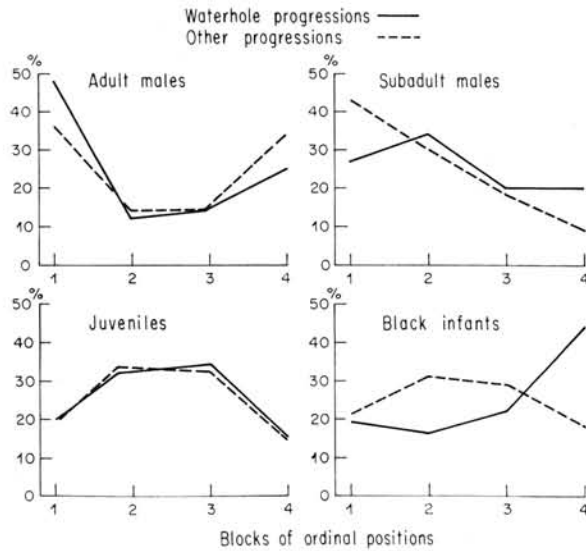


Fig. 7. Comparison of progressions approaching waterholes with all other progressions. In 4 blocks of successive ordinal positions, 1 is front and 4 is rear.

occasions, black infants were seen off their mothers near the water, but only after the area had been investigated.

In figure 7, waterhole progressions are compared with all others. Progression positions are grouped into four blocks instead of eight because only 16 waterhole progressions were recorded. This small n is a reason for caution in generalizing the waterhole data beyond the present case. Positioning in waterhole progressions appears different from positioning in other progressions for three of the four demographic classes. Compared to other progressions, there was a 12% shift to the front quarter in waterhole progressions of adult males. Of the identified animals, only the adult males were the first to approach waterholes, and among all troop members they were first 75% of the time. Subadult males and mothers carrying black infants shifted their positioning toward the rear. For the subadults, there was a 16% shift from the first quarter to the other quarters. The most striking change occurred for mothers carrying black infants, who shifted 26% from the front three to the rear quarter, without ever being last. The waterhole curve for riding black infants is based upon only 2 animals and 16 progressions; nevertheless, it is worth noting that, upon entry into many waterholes, the rearward position of black infants was probably among the least dangerous because the troop was moving towards cover

Formations of progressions approaching waterholes were recorded 15 times of which 93% were neat file or file formations; in comparison, the corresponding figure for all other progressions was 62%. The difference between these two percentages ($z=2.17$, $p=0.03$) suggests that file formations are more likely in moderately tense circumstances which are not frightening enough to cause precipitous flight.

Progressions Following a Severe Alarm

The ten successive neat file progressions upon which figure 1 is based occurred in response to a severe alarm near a waterhole located on the boundary of the KH woods and an open plain [see waterhole KH-3 in ALTMANN and ALTMANN, 1970]. The animals approached the waterhole from the plain where visibility was very good. The day was hot, and they filed in for a drink without slowing or compacting. After drinking had commenced, a mild alarm occurred and about six animals dashed away from the water for a moment, but shortly thereafter the troop was relaxed and a black infant off its mother was playing near the animals who had momentarily retreated. At approximately 17:40 h, the troop began to enter the KH woods heading toward a sleeping grove little-used in recent days and at which a juvenile had recently disappeared. As the troop rounded a clump of bush, two warthogs about 100 yd away began to run and vervet (*Cercopithecus aethiops*) alarm calls were heard. The troop suddenly turned and dashed back into the open plain. The source of fear was not seen by the observer. For 45 min, the troop first ran, then ran and walked, and then walked for a total of approximately 2.7 mi before reaching a sleeping grove which they often used [see grove 2a in ALTMANN and ALTMANN, 1970]. During this long trip, their initial fear reaction was probably sustained by their exposed position far from sleeping trees so late in the day. They took a circuitous route from the waterhole to the sleeping grove, skirting large clumps of bush and sticking to the open plain. Walking yearlings stayed close to their suspected mothers, and one infant-2 who normally walked rode ventrally on its suspected mother [HAUSFATER, personal commun.]. Upon arriving at sleeping grove 2a, the troop ascended into the trees without the socializing that usually occurred first.

Figure 8 shows the positions of adult males and black infants in each of the ten fear progressions. Movement was sometimes so rapid that not all known animals could be positively identified, in which case they were recorded either as 'adult male', or 'riding black infant', or not recorded at all. The data form a pattern in which adult males, as usual, were found mostly in the front or rear, and riding black infants were rather centrally located. There

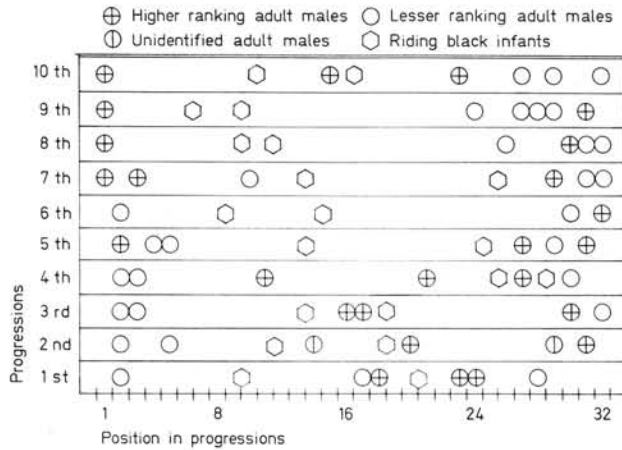


Fig. 8. Positioning of adult males and riding black infants in ten successive progressions following a severe alarm.

were always five or more animals in front of black infants, including at least one adult male and usually more, and there were always three or more animals behind black infants, including at least one adult male and usually several. During the first three progressions, at the height of the fear reaction, black infants and some dominant males were together near the center of the troop.

The long march from waterhole KH-3 to sleeping grove 2a underscores the reason for not defining progressions from a start to a stop and instead defining them as the flow across a point in the day's total line of march. Here was a case of uninterrupted movement with a distinct beginning at the point of a sudden reversal and a distinct end at sleeping trees. From the point of view of spatial organization, much information is lost if this start-to-end movement is sampled just once; indeed, to measure a start-to-end movement only once is an almost certain means of obtaining an incomplete and possibly misleading picture of its spatial organization. Such measures are best considered a single sample of a highly dynamic process. There is no one spatial arrangement characterizing a long trek; rather, constant interchanging of positions occurs within which certain patterns regularly reappear. Thus, figure 8 depicts black infants somewhat centrally located, but the actual positions they occupied varied considerably, with *Kub* in front of *Dogo* five times and behind three times (twice the two were not distinguished). Similarly, *Stubby*, who was first during the last four progressions, was otherwise in positions 24, 20, 16, 11, and 31 (once unknown). The ranges of known positions of all adult males in

figure 8 were 1-31, 2-31, 15-32, 2-32, 26-32, and 2-31, and the ranges of the two black infants were 6.5-25.5 and 9.5-28.5. An understanding of this degree of variation, which is not at all evident from figure 8, depends upon knowledge of identified individuals.

Speed of Movement

Estimates were made of the distance traversed from the troop's center of mass at the time when a progression began to the center of mass at the time when it ended. When using this distance measure, the observer's unaided estimate was made at the end of a progression, requiring his memory of the approximate location of the center of mass when the progression began. Therefore, the distance between centers of mass is a very gross measure, probably useful only for ordinal comparisons. For example, a distance between centers of mass estimated as 50 m was almost surely smaller than one estimated as 200 m even though the numbers 50 and 200 might be in error by a considerable amount. Furthermore, the distance between centers of mass was sometimes unduly lengthened because of a few animals starting well before the rest of the troop or because of a few stragglers. It might be better in the future to estimate the distance between centers of mass after some percentage of the lead animals have crossed the counting point and before a similar percent of the rearward animals have reached it.

The distance between centers of mass divided by the duration of the progression provides a gross estimate of relative speeds of movement for different formations, actions, and vegetation conditions. Five formation-action combinations were considered, as follows: (1) neat file with walking and/or running; (2) file with walking and/or running; (3) file with feeding (walking and/or meandering); (4) flank (including file-flank) with walking and/or running; (5) flank (including file-flank) with feeding (walking and/or meandering). The mean estimated meters of movement per minute was 26.26 for neat file progressions, all of which had walking and/or running actions. The means for the remaining formation-action categories are shown in table III, which is set up in the format of a two-way analysis of variance and which shows heterogeneous standard deviations. Using the basis for choice discussed by WINER [1962], a log transformation was chosen to reduce heterogeneity of variance, and a two-way analysis of variance was performed. There was neither a significant interaction nor a significant effect associated with type of formation. The difference between actions was highly significant ($F = 33.31$, d.f. = 1, 133, $p < 0.001$), which is hardly surprising. Neat file progressions were significantly faster by *t* test (d.f. > 30 in all cases) than other file progressions with walking

Table III. Movement (m/min) by formation and action

Action	File formation		Flank formation		Overall mean
	mean	SD	mean	SD	
Walk/run	17.08	13.67	21.16	14.63	19.12
Feeding and walk/meander	7.78	3.28	9.88	7.23	8.83
Overall mean	12.43		15.52		

and/or running ($t = 3.22$, $p < 0.01$), other file progressions with feeding ($t = 7.06$, $p < 0.001$), and flank progressions with feeding ($t = 6.42$, $p < 0.001$); neat file progressions were also faster than flank progressions with walking and/or running, but the difference was not significant ($t = 1.18$).

Progressions occurring in bush, open-bush, and open, have mean meters per minute of movement of 11.60, 17.41, and 17.69, respectively. These means differed ($F = 3.08$, $d.f. = 2, 174$, $p < 0.05$) due to slower movement in bush than in the other conditions. The fastest movement occurred in neat file progressions where the troop seemed to be moving away from one location and heading for an anticipated end point, as in the ten fear progressions, and the slowest movement occurred in bush where caution is especially compatible with survival. Progressions through bush may be slowed by a greater abundance of food and by feeding in trees. But whatever the reason for a slower pace, it improves the troop's opportunities to investigate the surrounding vegetation and lessens the chance of being surprised by a predator.

Discussion

Quite similar age-sex positioning in progression orders occurred across different species, troops, habitats, and studies. Such reoccurring order would be expected of a spatial arrangement thought to serve a protective function and thought to play an important role in baboon adaptation to a terrestrial existence. Considering the crude methods employed to assess spatial arrangements, further interesting relationships may be detected by using improved or different methods to study additional facets of spatial organization.

Protective Positioning

While there was evidence of nonrandom positioning by demographic class and even by individual, there was also evidence of considerable movement from one place in the progression order to another. The data indicate quite clearly a nonrandom distribution of age-sex positioning, having as its most striking feature a tendency for adult males to occupy front or rear positions. Nevertheless, the troop does not progress, like a formation of marching soldiers, with each individual in the same appointed place from start to end. Rather, there is a tendency toward the reoccurrence of certain patterns in a spatial order that is continuously rearranging itself as the troop moves forward.

Variation in progressions probably arises from several sources. The regulation of movement in space may arise from many of the same factors underlying the regulation of spatial relations in other aspects of group life, including intratroup aversions and attractions seen in fearful or confident behavior, and behaviors such as interest in infants, consort relations, and displacements. Variation may also occur because of physical factors such as age or injury. For example, *Sinister*, the adult male who most often lagged behind and least often moved near the front, was an older male who ran with stiff limbs. He often appeared tired by the middle of the afternoon at which time he was most likely to start lagging behind. Similarly, the adult male *Dutch*, who started near the head of the earliest of the ten fear progressions, appeared to tire, and by the tenth progression he was well behind the entire troop. Unpredictable, extra-troop events also introduce variations into the progression order. For example, high negative correlations occasionally occur between two successive progressions, as when Amboseli baboons spot approaching Masai tribesmen and do an about-face. Another unpredictable source of variation occurred after several of the ten fear progressions, when an adult female near the front chanced upon and caught a hare. The troop's premier meateater, the adult male *Ivan*, began harassing her, causing her to fall back from near the front to near the rear of the troop. More commonly, however, progression positions were interchanged undramatically without the observer being especially aware of the reason: One animal stopped to scratch himself and others walked by; another animal passed a grooming pair, stopped, and began to dig a rhizome, while still others passed him; a few animals climbed a tree to rest, look, or feed while others moved on; or several playing juveniles dashed back and forth among other group members as the troop moved along. An interesting source of progression variation is found in a statement of ROWELL [1969, p. 250]:

'Another difference between the two troops was that the males were more

sharply differentiated in position from female adults in V troop than in S [that is, adult males were more often first or last in V troop than in S]. V troop was usually counted across some sand flats next to a road which they always crossed with great caution after checking by the adult males for human traffic, and this probably explains why the males were more in the van at this point, and provides an illustration of the way in which spatial organization can change in response to external situations.'

It is suggested that the roots of the order found in the midst of progression variation can be largely attributed to differences in fearfulness among demographic classes. Fear varies in intensity, depending upon the arousal stimulus, and intensity is inferred from reactions ranging from confidence behavior, indicating fearlessness, to freezing or frenzied fleeing, indicating terror. Progressions tend to be occasions for increased nervousness or vigilance. Thus, KUMMER [1968] noted that the distance from hamadryas baboons (*Papio hamadryas*) at which an observer was tolerated without flight increased from resting to marching. And among geladas (*Theropithecus gelada*), all-male groups were found mainly at the front of the herd, moved faster than units with females, and appeared to possess a 'less nervous disposition' than units with females and young [CROOK and ALDRICH-BLAKE, 1968].

Nature and experience should combine to yield bolder behavior from adult males than from other troop members. Even the preadolescent male appears to be more rambunctious than females of the same age, as indicated in macaques and baboons by the female's earlier withdrawal from rough and tumble play [e.g., BLURTON-JONES, 1967; DOLHINOW and BISHOP, 1972; HARLOW *et al.*, 1971; RANSOM and ROWELL, 1972; SIMONDS, 1965]. By 6 months of age, male rhesus (*Macaca mulatta*) were already threatening more and exhibiting passive avoidance less than their female counterparts, and these differences occurred in animals who had no opportunity to learn from older monkeys [HARLOW and ROSENBLUM, 1971]. The adult male more than others is likely to have had experience on the spatial fringes of the troop as a young peripheral male, as an outsider, or as an occasional loner. By the time a male reaches adulthood he should and does behave more confidently than other group members in respect to extra-group conditions or events. By the same token, more fearful group members should have learned the advantage of situating others between themselves and possible danger. Probably the least confident animals are the walking young who have not yet achieved the independence and experience that instills confidence; consequently, as the data indicate, 'Juvenile play groups will not wander far from the troop's center' [DEVORE and WASHBURN, 1963, p. 342].

DEVORE and WASHBURN [1963] noted that the boldest troop members were situated near the front and rear of progressions; only the less dominant and older juvenile males were mentioned as boldest, but it seems reasonable to include all adult males in this category. KUMMER's [1968] description of movements of hamadryas and CROOK's [1966] description of geladas also indicate positioning of adult males primarily at the front or rear of their groups. Differences in extra-troop boldness among adult males should be related in part to age and strength. The subadult and prime males tended confidently to move near the front, while the older males with less stamina, who had ample opportunity to learn to pace themselves, tended toward the rear of the troop. There may also be a propensity for some older or subordinate males to leave a goodly amount of space between themselves and some frontal males; detailed knowledge of relationships among individuals is needed to check this hypothesis.

The more fearful troop members may contribute to the positioning of the bolder individuals by avoiding the front and rear. The more cautious troop members would be expected to keep other animals between themselves and potential danger. An area of potential danger, and therefore of fear, is the uninvestigated area into which a moving troop is headed. For example, 'A troop which is coming toward trees from the plains approaches with particular caution' [DEVORE and WASHBURN, 1963, p. 343], and similar caution is displayed when heading into waterholes. There may also be fear of falling behind or being surprised from behind. Thus, the least bold troop members, who are probably walking infants and younger juveniles, would tend to avoid the front and rear of the troop.

Adult females, being neither the most nor the least fearful, would tend to be spread across front, middle, and rear progression positions, perhaps depending more upon propensities of individuals than upon properties of the demographic class. The progression positions of riding black infants are necessarily similar to those of their mothers, and available evidence indicates that mothers with black infants do not usually position themselves in progressions very differently from adult females as a whole [HARDING, 1973]. Mothers carrying infants may gravitate toward the troop's center in very frightening situations, as they did during the ten successive fear progressions, but further data are needed to check the generality of this reaction.

Instances have been reported of males interposing themselves between the troop and potential danger [e. g., ALTMANN and ALTMANN, 1970; DEVORE and WASHBURN, 1963; ROWELL, 1966; STOLTZ and SAAYMAN, 1970]. On the other hand, a strong fear stimulus can produce 'precipitate flight with the big males

well in the front and the last animals usually the females carrying heavier babies' [ROWELL, 1966, p. 362]. STOLTZ and SAAYMAN [1970] observed a similar flight pattern. It seems quite probable, as ROWELL suggests, that the order of movement in these situations depends upon the degree of fear. When males are very frightened they will run, but if they are not, either the running of the less bold animals past them will leave the males interposed between the fear source and the rest of the troop or will leave the males to attack animals, such as dogs [STOLTZ and SAAYMAN, 1970] whom they are able to kill or maim.

Differential reactions of males and other troop members to danger are consistent with the hypothesis that fearfulness or confidence is a main determinant of differences in progression tendencies among demographic classes. Normal individual differences or the behavior of occasional aberrant animals are also consistent with this hypothesis. For example, if a particular adult male is unusually fearful and cautious, it is expected that he would be found less often near the front or rear. Similarly, an aberrant juvenile who has little fear of extra-troop events should be seen more often than his peers near the front or rear, which would likely reduce his chances of surviving to pass on any genetic basis of his aberrant behavior.

Dyad Distances

The ordinal position of movement across a counting point no doubt gives some information about who is near whom, but it also leaves much unsaid, as two examples will illustrate. First, suppose three animals cross first, fifth, and fifteenth in a file progression. It is not only possible for the first and fifth animals to be much further apart than the fifth and fifteenth, it was in fact sometimes the case when a lead animal moved well in advance of the remaining troop members. Second, suppose there is a flank progression in which three animals cross first, second, and last. If the first and second animals happen to be on opposite ends of a long flank, they may be further apart than the first and last.

Evidence relevant to a protective theory of spatial organization need not be limited to the order of march. Indeed, if it is, a seeming contradiction emerges. On the one hand, some evidence indicates a spatial affinity between adult males and young [DEVORE and WASHBURN, 1963; RHINE and OWENS, 1972; STOLTZ and SAAYMAN, 1970]; but on the other hand, no such affinity was found in studies of progression order in which males tended toward the front and back and small juveniles and black infants did not. However, even within this spatial arrangement, the distance between vulnerable young and an adult male might be less than the distance between other animals and a

male. Every male does occasionally occupy all progression positions. It is possible that several vulnerable animals will tend to cluster around those few males who happen to be near the troop's center at any given time. This possibility can be checked by determining the nearest neighbors of identified troop members or by determining distances among identified pairs of animals. Neither the nearest-neighbor measure nor distances among pairs of animals are obtainable from the censusing techniques used so far to study progressions. In order to make optimum use of nearest-neighbor or other distance data, it is desirable to know dominance relations and social affinities among members of a troop, all of whom are individually identified.

The distance between animals, unlike virtually every other important social behavior, has the methodological and comparative advantages of occurring on every occasion of any rational sampling method and of being applicable by the same fundamental scale of measurement to all species. The sociogram of distances among members of a troop probably provides as close an approximation of the overall pattern of approach and avoidance tendencies as does any other available index. Spatial measures make possible within-troop comparisons under different conditions, such as rest versus movement or relaxed versus tense conditions. Hence, distances at one and the same time provide useful information both about social affinities and about possible protective positioning by demographic class. Distance data are also important in methods used to identify and analyze the social organization of animals clustered into subgroups, [e. g., ALDRICH-BLAKE *et al.*, 1971; KUMMER, 1968; NAGEL, 1971; RASMUSSEN, 1973].

Subgroups

Any protective spatial arrangement occurring either between or within temporarily separated subgroups would not be detected with the censusing techniques employed at Amboseli and elsewhere. On several occasions it became necessary to cancel a progression because a subgroup went off in a direction that did not cross the established counting point. In all such cases, the subgroups contained at least one adult male. Similarly, the separately foraging hamadryas harem unit always contains an adult male, and the two-unit initiator-decider group of this species contains two males, one of whom typically moves in the front of the group while the other brings up the rear [KUMMER, 1968]. The presence of adult males in separated parties puts less powerful animals at a disadvantage in competition over food. Disregarding protection and considering food intake only, females and young would be better off in subgroups without adult males; yet, separated baboon subgroups

devoid of adult males virtually never occur in nature. KUMMER [1968] suggests that the one-male hamadryas unit evolved to maximize foraging effectiveness by spreading subgroups across sparse feeding areas. At the same time, protection is maintained by the presence of at least one adult male in each foraging group. Potentially revealing questions are posed by consideration of age-sex variation in the spatial arrangement of subgroups. For example, to what degree do vulnerable young (or others) tend to leave the main body of the troop and travel in subgroups? Do they remain closer to adult males in subgroups than in other groups? And do subgroups with many vulnerable young tend to stay closer to the main body of the troop than do subgroups with few or no young?

Decreased Inter-Animal Spacing

Substantial decreases in space between animals appeared to occur in response to external sources of moderate tension. Thus, ALTMANN and ALTMANN [1970] listed seven actually or potentially threatening situations among eleven circumstances in which compaction occurred. The compacting pictured in figure 1E was seen far from trees and in the midst of high grass (*Sporobolus robustus*) near which baboons are often alert or tense [ALTMANN and ALTMANN, 1970]. The reason for close compacting in this case was not known. On another occasion, the troop was approaching a waterhole. After those in front had stopped, the entire troop moved into an unusually tight cluster similar to the one illustrated in figure 1E, and remained that way for several minutes while signs of tension mounted around them. At one point an impala herd ran off, and shortly thereafter two elephants dashed away from the scene. When Masai herdsmen with cattle appeared, the baboons remained packed together and watched the cattle pass perhaps 100 m away. Only then did the animals disperse as they began filing toward the waterhole.

Summary

The order of movement in progressions of yellow baboons was analyzed in terms of the possible protective function of spatial organization, and compared to the order of movement of anubis baboons. Similar nonrandom positioning occurred in different troops, species, habitats, and studies. Such positioning was consistent within demographic classes and differed across classes. More complete spatial data would be useful in further investigations of the organization of progressions.

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