

THE SOCIO-SPATIAL ORGANIZATION OF BABOON (*PAPIO CYNOCEPHALUS*) PROGRESSIONS AT MIKUMI NATIONAL PARK, TANZANIA

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The socio-spatial organization of Baboon (Papio cynocephalus) progressions at Mikumi National Park, Tanzania.—In the pioneer research of Washburn and DeVore, the socio-spatial organization of moving baboon progressions was thought to serve a protective function. The large, powerful adult males provided an outer ring and an inner core of protection to centrally located, vulnerable young. A series of studies conducted at Mikumi National Park has been aimed at evaluating a modified form of the protection theory. In the present paper, the Mikumi findings are reviewed, supplemented, and placed in the context of related research from other baboon field sites. The Mikumi data diverged somewhat from those of early reports, but they were consistent with the modified theory and with main themes of the original protection theory.

Key words: Progression order, *Papio*, Protection, Males, Immatures.

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INTRODUCTION

Over twenty years ago, Washburn and DeVore published a series of papers which were destined to fuel the then fledgling science of fields primatology as few have done before or since (e.g., DEVORE, 1964; DEVORE & WASHBURN, 1963; WASHBURN & DEVORE, 1961a, 1961b). These papers served to guide a small army of budding primatologists into field studies of primate ecology and behavior, both to develop more fully and to examine critically the ideas which emerged from the pioneer research. Among these ideas, none received more attention than hypotheses about the possible protective function of the socio-spatial organization of a baboon troop as it moves from one location to another (fig. 1). As ALTMANN (1979) pointed out, the progression order observed by Washburn and DeVore "can be described without exaggera-

tion, as the most widely known claim for an adaptive group geometry that has been made for any animal [p. 47]."

Washburn and DeVore observed a spatial organization in which the most vulnerable animals, the small infants, were centrally located, surrounded by other troop members, including two tiers of powerful adult males. An adult male baboon is approximately twice the size of an adult female, and he possesses huge canine fangs capable of inflicting serious wounds upon any but the strongest and most persistent predators. Several baboon males acting in concert are formidable opponents which few predators will dare to challenge. Protection was thought to be provided by prime dominant males near the vulnerable young in the core of the troop and by the less dominant adult and subadult males at the troop's periphery.

Washburn and DeVore's hypothesis about the protective function of progression

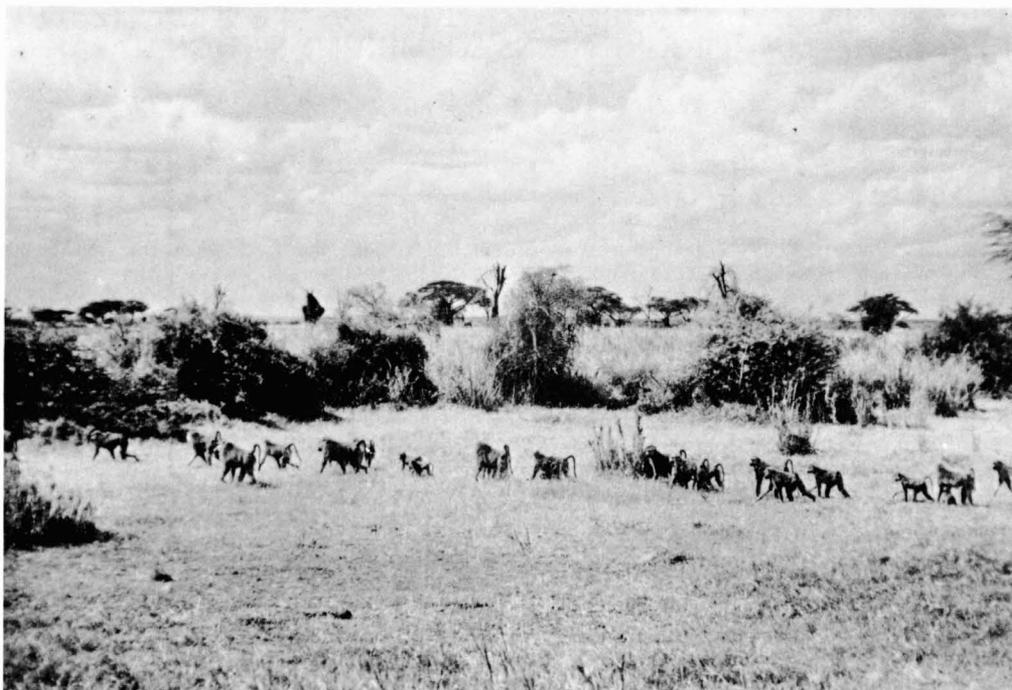


Fig. 1. A progression of yellow baboons (RHINE, 1975).
Progresión de babuinos en movimiento (RHINE, 1975).

patterns has been the subject of studies at Mikumi National Park and elsewhere. The present paper is a review of such progression research, concentrating upon the Mikumi studies, which are among the most detailed and complete and which are based upon the largest available sample of progressions and of animals of all age-sex classes. In Mikumi research, progressions from two yellow baboon (*Papio cynocephalus*) troops of different size were studied over a period of several years. The findings are reviewed within the context of progression research from several other baboon sites, which are the east and southern Africa locations of three species of common baboons, yellow, olive (*P. anubis*), and chacma (*P. ursinus*). These findings can be used to evaluate the original form of the protection theory and to suggest modifications which improve the fit between data and theory.

Implications of the protection theory

In the most general sense, leaving aside the specifics of the Washburn and DeVore formulation, the protection theory has five main themes (RHINE, 1975). First, the theory implies that the order of progressions is nonrandom, and second it is a non-random order which tends to protect the vulnerable young. Third, adult males will tend to occupy progression positions which place them between vulnerable young and predators (see HAMILTON'S, 1971, discussion of the selfish herd). Fourth, the protection theory is an ultimate theory in which progression order is thought to be an outcome of the baboon's evolutionary history. And, therefore, fifth, an appropriate non-random order should tend to recur persistently despite variations in habitat, baboon species, troop size and composition, and research procedures.

Modified and expanded protection theory

The Mikumi research reported here was undertaken to evaluate a modified and expanded form of the protection theory. Two initial studies (RHINE, 1975; RHINE & OWENS, 1972) served as pilot projects, and based upon them the original protection theory of Wasburn and DeVore was reconsidered. Four main changes or additions were incorporated into the theory.

First, the most dangerous part of moving progressions were assumed to be the front and rear. Because the vanguard of a moving troop is entering areas the animals have not yet had an opportunity to explore, individuals at or near the front of the troop are taking a chance on being ambushed. Thus, BUSSE (1980) reported that lions at the Moremi wildlife Reserve waited in ambush to attack baboons moving toward them. Similarly, lagging behind attenuates the protective conditions available to animals nearer to the troop's center of mass, where vigilance and defense is more likely to be a multi-animal undertaking.

Second, the walking rather than the riding young are considered to be the most vulnerable animals. Left to their own devices, the smallest infants would no doubt be the most vulnerable; however, a small infant rides on its mother in progressions, so it constantly receives the benefit of her strength, experience, and psychological support without which it is unlikely to survive (RHINE, NORTON et al., 1985). For example, a four month old female infant from a Mikumi troop was unable either emotionally or physically to keep up with the troop after her mother died. Instead of moving with the troop, she stayed behind and screamed. At one point, before an adult male returned to retrieve her, the troop was out of sight 500 m away and the infant was wandering aimlessly by herself in tall grass (RHINE, NORTON et al., 1980). When infants first begin foraging and traveling on their own, they are still quite small and inexperienced. Yet, infants in the second six months of life are often out of sight of their mothers. When

away from its mother, a walking infant or small juvenile is probably the most vulnerable animal in the troop. It would be easy prey even for small felids or canids, such as jackals, if left on its own. Interestingly, when juveniles and jackals come together while in the midst of troop adults, the jackals make no attempt to take the small baboons (SAAYMAN, 1970), presumably because of the restraining effect of nearby troop members. Sometimes jackals or other small predators may be chased off by adolescents and adult females (STEIN, 1984).

Third, it is assumed that, among many possible proximate causes of progression positioning, a key one is fear or confidence. Fear or confidence is a function of physical strength, maturation, temperament, and experience. Small, inexperienced animals are probably the least confident troop members, and are likely to be fearful of being too far from other members. Therefore, they are expected to maintain spacing which allows them readily to place other troop members between themselves and potential danger and to receive assistance from older animals (HAMILTON, 1971; BUSSE, 1984). The most confident troop members should be the adults, particularly the adult males who have experienced their own size and strength, who sometimes spend days by themselves (SLATKIN & HAUSFATER, 1976), and who typically transfer from one troop to another (PACKER, 1975, 1979; RASMUSSEN, 1981).

Fourth, it seems probable that the basic protective ordering rather than being rigid, will bend in response to specific social or ecological conditions. HARDING (1977) cited comments of several observers, including Washburn, who "have noted that baboon troops behave differently in different parts of their range [p. 352]." Baboons are long-lived, highly intelligent animals capable of learning adjustments which may differ from troop to troop and from one situation to another. For example, in progressions into waterholes, which support bush that can hide predators, the adult males might be even more forward than usual and females carrying infants

might tend to lag toward the year (RHINE, 1975; RHINE & WESTLUND, 1981).

PROCEDURES

In the early days, socio-spatial information was determined from qualitative impressions of whole troops by keen observers who were also attempting to attend to a variety of other key aspects of ecology and behavior. Not long thereafter, ROWELL (1969) introduced the simple procedure of determining by age and sex the order of movement as the troop flowed past a counting line, and this procedure has been the essential starting point of all quantitative studies which followed. She and many who followed her collected progression data while censusing troops. For some of these troops, all individual members were identified and the troops were well habituated to observers, but sometimes neither of these conditions prevailed. Without good habituation for close up observation, even broad age-sex class, the essential variable for tests of the protection theory may be difficult to establish accurately. Without individual identification, it is next to impossible to apply to the data standard statistical tests for which the basic assumptions are satisfied. Individuals of the two Mikumi study troops, Viramba and Mgodia, were habituated and identified.

Variations among procedures persist, and in some cases, procedures are too insufficiently described to evaluate fully their appropriateness; still, the basic procedures in recent studies were designed to establish age-sex order. At Mikumi, this order was recorded by a team of two observers. One observer spoke into a tape recorder the name of each identified individual as it passed a line of sight to a stationary object such as a tree. The other observer was able to move about and to take his eyes off the counting line. He noted animals which might otherwise be missed and helped determine identifications. If an animal crossed back over the counting line, it was counted only on the final crossing. If an

animal could not be identified, as when many crossed the line very rapidly, an attempt was made to identify animals only by age-sex. If that failed, as it occasionally did, the animal was described only as "other" to maintain the correct order of identified individuals. Recently, in addition to order of movement, some researchers have begun to look at other aspects of the spatial organization of moving troops (BUSSE, 1984; COLLINS, 1984; Norton, pers. comm.). While these studies usefully supplement progression research, so far they are not crucial for evaluation of the main tenets of the protection theory.

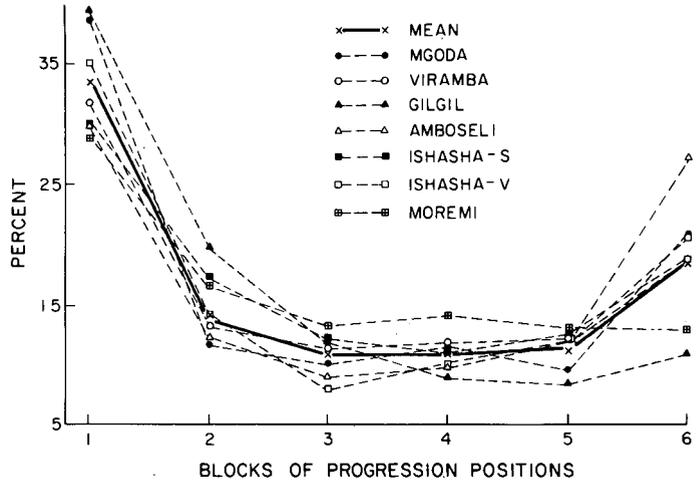
RESULTS AND DISCUSSION

Adult males

The most critical age-sex class for the protection theory is adult males. If these animals were randomly distributed across progression orders and in relation to other age-sex classes, it would be very difficult to advocate the theory convincingly. Data from several studies of progression order of *P. cynocephalus*, *P. anubis* and *P. ursinus* are fully consistent in one respect: in every such troop, adult males progressed in a non-random order (ALTMANN, 1979); COLLINS, 1984; HARDING, 1977; ROWELL, 1969; RHINE, 1975; RHINE & WESTLUND, 1981; RHINE, BLOLAND et al., 1985). Whenever it was possible to conduct strong statistical tests of this ordering, the results were statistically significant. The finding of non-random order of adult males is persistent and unequivocal to a degree possibly unprecedented in field primatology.

The ordering of adult males is shown in figure 2 where sixths of progression positions are on the abscissa, i.e., one is the front sixth of a progressing troop and six is the rear sixth. The points on the curves are the mean percent of progressions in which males of a given troop were in each sixth. In all of the seven troops depicted, the adult males tended to occupy the frontal positions. Figure 2 shows that in some cases there was a secondary ef-

Fig. 2. Mean percent of progressions during which adult males of seven troops were in each of six blocks of progression positions (RHINE, BLOLAND et al., 1985). Front is 1 and rear is 6. Viramba and Mgoda troops are yellow baboons from Mikumi; the Amboseli troop is yellow baboons from Amboseli National Park in Kenya. The Ishasha troops are olive baboons from Queen Elizabeth National Park in Uganda; the Gilgil troop is olive baboons from a ranch near the town of Gilgil in Kenya; and the Moremi troop is chacma baboons from the Moremi Wildlife Reserve in Botswana.



Porcentaje medio de progresiones durante las cuales los machos adultos de siete grupos estaban en cada una de las seis posiciones posibles de una progresión (RHINE, BLOLAND et al., 1985). La parte anterior está marcada con un 1 y la posterior con un 6

fect in which adult males were found also toward the rear of the troop. Although not illustrated in the figure, the dominant males tended to be frontward more than subordinates (HARDING, 1977; RHINE & WESTLUND, 1981). In addition, several studies show that the very first or the very last troop member was an adult male significantly more often than expected on the basis of group composition, an effect which is particularly strong for the lead position of the troop (RHINE & WESTLUND, 1981; RHINE, BLOLAND et al., 1985).

Further analyses address the generality of the results. Of the 46 cases from several sites where males were individually identified, 39 were overrepresented either in the front or rear, a result which would occur by chance less than one time in a trillion. A variety of analyses have been performed to determine if the progression order of figure 2 changed significantly in different circumstances. There was one exception, but otherwise the frontal tendency occurred in virtually all habitat variations that have been investigated to date, such as leaving sleeping trees or moving

through open versus bushy country (RHINE, 1975; RHINE & WESTLUND, 1981). Similar consistency occurred for the progression positioning of other age-sex classes reported below.

The exception to the usual frontal positioning of adult males is a case which seems to prove the rule. When a troop is moving away from a frightening situation, the rearward tendency may be exaggerated at the expense of the more common frontal positioning. For example, Tilson (pers. comm.) recorded two progressions of chacma baboons while the observed troop was being supplanted by another. When these two cases were compared to other progressions of the same troop, the adult males were seen to lag toward the rear where they were between the foreign troop and members of their own. Similarly, ALTMANN (1979) and RHINE (1975) reported a tendency toward increased peripheralization in frightening circumstances, and these researchers have also found an increase in male frontal positioning when a troop enters a waterhole which could hide predators (RHINE & WESTLUND, 1981).

An additional indicant of consistency is a comparison between the findings of RHINE (1975) and ALTMANN (1979) who studied the same seven adult males. This comparison is particularly noteworthy because Altmann attaches little credence to the protection theory. Yet, his data, analyzed and published after Rhine's, are a remarkably excellent replication of the frontal and rearward tendency (RHINE & WESTLUND, 1981). Altmann used thirds of progression patterns instead of sixths. Table 1, which is an overall comparison of his and Rhine's data, shows that adult males were in the front third most often, the rear third next most often, and the middle least often, and the percentages from the two studies are quite similar. Since this replication held also on an animal by animal basis, it is probably among the closest replications of quantitative data yet produced from baboon field studies (RHINE & WESTLUND, 1981).

Walking infants and small juveniles

In addition to adult males, two other age-sex classes of particular interest for the protection theory are the infants and small juveniles. Without protection, these small animals would be easy prey for predators. A newborn baboon has black hair. It gradually turns to the adult color for which yellow and olive baboons are named. A small black infant almost always rides on its mother during its early months of life, but a transitional infant of approximately six to twelve months of age often walks on its own (RHINE et al., 1984).

Since the positioning of a riding infant is the same as its mother's, attention here is turned to the walking infants and small juveniles. Figure 3 shows the progression positioning of walking infants (less than twelve months of age), and figure 4 shows similar data for small juveniles (1 to 2.5 years of age). It will be seen from these two figures that the small walking young tend to be centrally located. This is consistently so for several troops of two species living in different habitats. Walking infants were underrepresented

Table 1. The mean percent of times adult males occupied the front, middle, or rear thirds of progression positions in two studies of the same seven animals (ALTMANN, 1979; RHINE, 1975).

Porcentaje medio de ocasiones en que los machos adultos ocuparon los tercios delantero, medio o trasero de las posiciones de progresión en dos estudios de los mismos siete animales (ALTMANN, 1979; RHINE, 1975).

Study	Progression positions		
	Front	Middle	Rear
Altmann	41.77	21.12	37.11
Rhine	43.15	20.19	36.66

mostly in the frontal sixth of progressions.

Small juveniles and walking young were also underrepresented in the lead position (RHINE, HENDY et al., 1980; RHINE et al., 1981). The lead position of progressions was analyzed for 82 walking infants from three locations, 11 troops, and two species. These data are from three studies involving several observers and somewhat different procedures. "Despite so many different opportunities for variation, 1317 observations from these 11 troops did not produce a single instance in which a walking infant led the troop and very few in which one was in the frontal twelfth" (RHINE, HENDY et al., 1980). This evidence alone provides strong confirmation of non-random progression order.

Adult females with and without riding infants

Figure 5 shows females progression positioning in six troops. The solid curve is the mean of the five troops for which sixths of progression positions were available. The points on the curve of means are not statistically different from each other. Nevertheless, the slight bow shape is consistent for all except the smaller of the two Mikumi troops (Mgoda troop). For the remaining four troops, there are no reversals in the trends, i.e., they drop consistently a low from which they then consistently rise. Overall, however, the differences between sixths seem too slight to relate in

Fig. 3. Mean percent of progressions during which walking infants of four toops were in each of six blocks of progression positions (RHINE, HENDY et al., 1980). Conventions as in figure 2.

Porcentaje medio de progresiones durante las cuales las crías que andan de cuatro grupos, se hallaban en cada uno de las seis posiciones de la progresión (RHINE, HENDY et al., 1980).

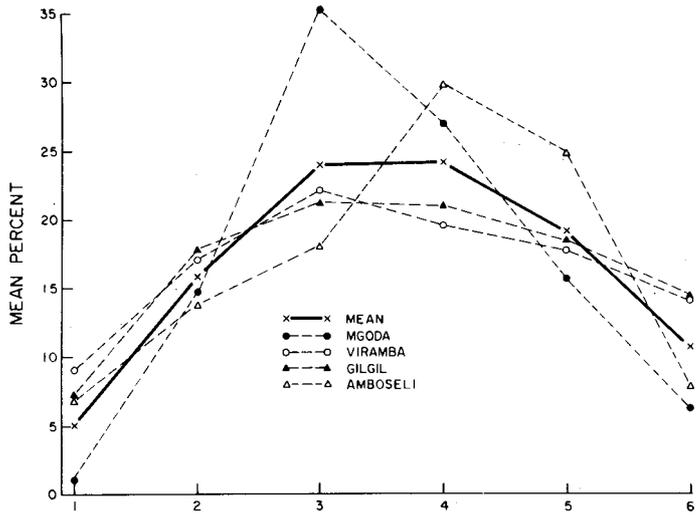


Fig. 4. Mean percent of progressions during which small juveniles of six troops were in each of six blocks of progression positions (RHINE et al., 1981). Conventions as in figure 2.

Porcentaje medio de progresiones durante las cuales los individuos juveniles de seis grupos estaban en cada una de las seis posiciones de la progresión (RHINE et al., 1981).

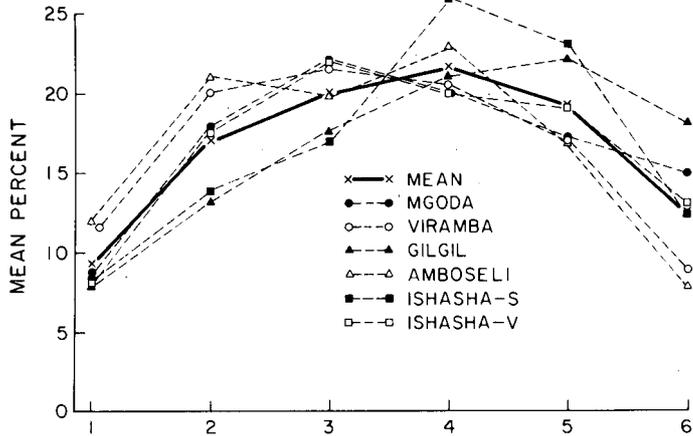
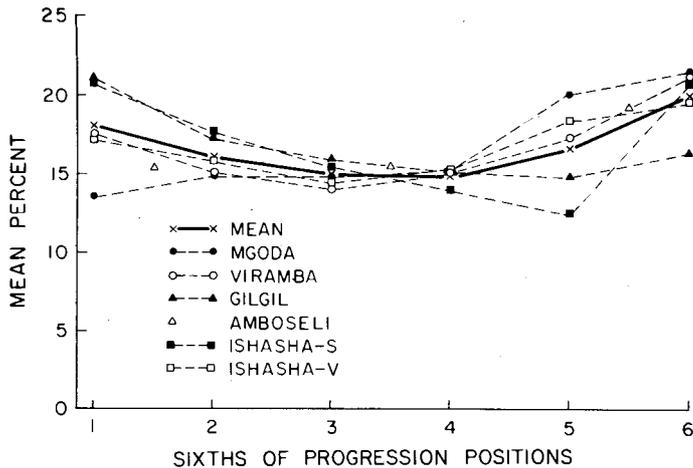


Fig. 5. Mean percent of progressions during which adult females of five troops were in each of six blocks (and in one case, three) of progression positions. Conventions as in figure 2.

Porcentaje medio de progresiones durante las cuales las hembras adultas de cinco grupos estaban en cada uno de los seis bloques (y en un caso de tres) de posiciones de la progresión.



a convincing way to the protection theory.

Figure 5 is based upon all females sampled, including those with and without riding infants. Statistically non-significant differences also occurred between females with and without riding infants. Mothers with riding infants tended to be a little more rearward. Younger infants rode ventrally and older, heavier ones sometimes rode dorsally, jockey style (RHINE, et al., 1984). Although the differences again were not statistically significant, there was a slight tendency for mothers with ventrally riding infants to lag behind in progressions, possibly because more recent mothers have not yet fully regained their strength after childbirth.

When attention is shifted from progression sixths to the first and last progression position, the rearward tendency of females comes more sharply into focus. First and last data are available for both Mikumi troops, and in both cases adult females were last significantly more often than expected on the basis of their numbers in the troops. In addition, adult females of both troops progressed less than expected in the first position. Adults of either sex or subadult males almost always occupied the first progression position (96% of the time for Viramba troop and 87% for Mgodá). They also occupied the last position more often than expected by chance.

Older immatures

If the progression positioning of adults is different from that of small juveniles and walking infants, then an orderly developmental transition would be expected from youth to adulthood. Furthermore, if males and females tend toward different adult positioning, then the developmental transition should be different for males than for females. Developmental effects and sex differences in developmental processes are of particular interest because they represent biological processes through which evolutionary forces underlying the protection theory may work.

Data on sex differences of large juveniles (2.5 years to female sexual cycling or to male

subadulthood) are available for identified individuals of two Mikumi troops (RHINE et al., 1981). Sex differences in the progression positioning of large juveniles is evident from figure 6. The intersecting curves are a classical form of statistical interaction, which in this case is significant at well beyond the .001 level. By the time they were large juveniles, males were tending more toward the front of progressions and females were tending toward the rear. These tendencies were apparent also in curves of progression positioning for individual animals. Of 40 large juveniles, the ten most frontward were males and nine of the ten most rearward were females. Similar analyses of small juveniles show the same trend toward a sex difference in positioning, but to a lesser degree, as would be expected in a development sequence.

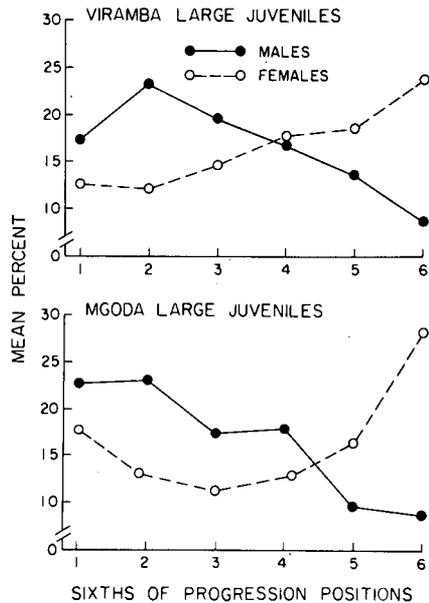


Fig. 6. Mean percent of progressions during which large male and female juveniles of two Mikumi troops were in each of six blocks of progression positions (RHINE et al., 1981). Conventions as in figure 2.

Porcentaje medio de progresiones durante las cuales machos adultos y hembras jóvenes de dos grupos de Mikumi estaban en cada uno de los seis bloques de posiciones de la progresión (RHINE et al., 1981).

The frontward trend in figure 6 for large juvenile males is more pronounced by the time of subadulthood (a male at least as large as an adult female, but not yet an adult male). Figure 7 is based upon four troops and two species living in three locations. Data from 14 identified subadults are available from three of these troops (RHINE et al., 1979). In 13 of these 14 cases, the individual curves of progression positioning show a clear frontward tendency, a result which would occur by chance less than once in a million trials. Like adult males, subadults were over-represented in the front sixth of the progression order, but unlike adults, subadults were not consistently over-represented in the lead position. For two of four troops, subadults were first more than expected by chance, and for the other two they were first in approximate proportion to their numbers in the troop (HARDING, 1977; RHINE, 1975; RHINE et al., 1979). The secondary tendency of adult males to bring up the rear (fig. 2) did not appear for subadults. ALTMANN et al. (1977) found that males reaching young adulthood rapidly rose in the dominance hierarchy. The lack of a secondary rearward trend in subadults and the elevated dominance ranks of young adult males probably represent a transition to the tendency of dominant adult males to be more frontward than subordinates (HARDING, 1977; RHINE & WESTLUND, 1981).

The developmental trend from walking infant to subadult is summarized in table 2. The

Table 2. Means of individual correlations between sixths of progression positions and percent of times in each sixth, for four classes of immatures categorized by sex (RHINE et al., 1981).

Media de correlaciones individuales entre sextos de posiciones de progresión y porcentaje de veces en cada sexto, para cuatro clases de inmaduros categorizados por su sexo (RHINE et al., 1981).

Age	Sex	
	Male	Female
Walking infants	0.02	0.27
Small juveniles	-0.18	0.16
Large juveniles	-0.61	0.27
Subadult males	-0.73	

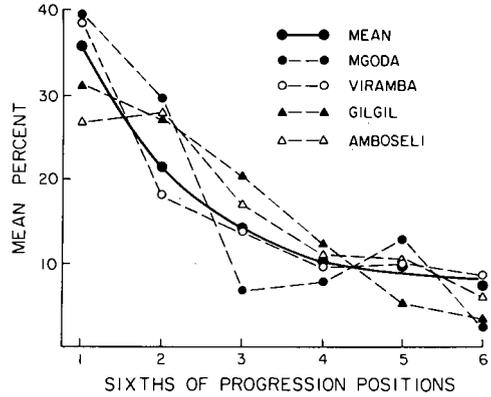


Fig. 7. Mean Percent of progressions during which subadult males of four troops were in each of six blocks of progression positions (RHINE et al., 1979). Conventions as in figure 2.

Porcentaje medio de progresiones en las que machos subadultos de cuatro grupos estaban en cada uno de los seis bloques de posiciones de la progresión (RHINE et al., 1981).

entries in table 2 are means of correlations obtained in the following manner. A graph of progression positioning was plotted for each of 20 identified walking infants, 33 small juveniles, 40 large juveniles and 14 subadults. These graphs were in the same form as figures 2 to 7. The correlation between percent (ordinate) and progression sixth (abscissa) was obtained. Such correlations will be negative for a frontward trend, positive for a rearward trend, and zero for no trend (a horizontal regression line). The higher the correlation, the stronger the frontward or rearward trend.

Table 2 shows a developmental increase in the frontal trend for males. Whereas male walking infants were neither frontward nor rearward (mean r of 0.02), the subadults were primarily frontward (mean r of -0.73). The small and large juveniles fit consistently between the youngest and oldest immature males. On the other hand, the immature females tended slightly toward the rear at all of the developmental levels, and exhibited no clear-cut developmental trend. There appears to be both a male developmental change and a sex difference in the progression positioning of immatures.

CONCLUSIONS

The findings reviewed in this paper are consistent with the modified protection theory. The order of progressions is clearly non-random. Adult males occupied the exposed frontal part of progressions and to a lesser degree the rear. Adult and large juvenile females were rearward more often than expected from chance, white subadult and large juvenile males were somewhat frontward. That leaves the troop's center as the primary domain of the least experienced and most vulnerable young, the walking infants and small juveniles. The results persistently recurred across several troops, species, habitats, and studies. Progression positioning was associated with developmental changes and sex differences resting upon biological processes susceptible to evolutionary molding (RHINE et al., 1981; RHINE & WESTLUND, 1981). The primary difference between the findings reviewed here and the initial observations of Washburn and DeVore are that dominant males were frontward rather than central and mothers with riding infants were not found primarily in the troop's center. The main themes of the original theory – including non-random positioning, the protective nature of the socio-spatial pattern of progressions, and the hypothetical adaptive origin of socio-spatial patterning – apply both to the original and modified versions of the theory. The data are consistent with these themes.

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SUMMARY

In the pioneer research of Washburn and DeVore, the socio-spatial organization of moving baboon progressions (fig. 1) was thought to serve a protective function. The large, powerful adult males provided an outer ring and an inner core of protection to centrally located, vulnerable young. A series of studies conducted at Mikumi National Park has been aimed at evaluating a modified form of the protection theory. In the present paper, the Mikumi findings are reviewed, supplemented, and placed in the context of related research from other baboon field sites.

The findings reviewed in this paper are consistent with the modified protection theory. The order of progressions is clearly non-random. Adult males occupied the exposed frontal part of progressions and to a lesser degree the rear (fig. 2, table 1). Adult and large juvenile females were rearward more often than expected from chance (figs. 5, 6), while subadult and large juvenile males were somewhat frontward (figs. 6, 7). That leaves the troop's center as the primary domain of the least experienced and most vulnerable young, the walking infants and small juveniles (figs. 3, 4). The results persistently recurred across several troops, species, habitats, and studies. Progression positioning was associated with developmental changes and sex differences (table 2) resting upon biological processes susceptible to evolutionary molding (RHINE et al., 1981; RHINE & WESTLUND, 1981). The primary differences between the findings reviewed here and the initial observations of Washburn and DeVore are that dominant males were frontward rather than central and mothers with riding infants were not found in the troop's center more than elsewhere. The main themes of the original theory – including non-random positioning, the protective nature of the socio-spatial pattern of progressions, and the hypothetical adaptive origin of socio-spatial patterning – apply both to the original and modified versions of the theory. The data are consistent with these themes.

RESUMEN

Organización socio-espacial de las progresiones de babuino (*Papio cynocephalus*) en el Parque Nacional de Mikumi, Tanzania. — En la pionera investigación de Washburn y DeVore, se consideró que la organización socio-espacial de las progresiones de babuinos en movimiento (fig. 1) tenía una función protectora. Los machos grandes y fuertes proporcionaban un anillo exterior y un núcleo interior de protección a los jóvenes vulnerables situados centralmente. Una serie de estudios llevados a cabo en el Parque Nacional de Mikumi ha tenido como fin evaluar una forma modificada de la teoría de la protección. En este trabajo, los datos de Mikumi se revisan, complementan y sitúan en el contexto de investigaciones similares llevadas a cabo en otras localidades con babuinos.

Los datos revisados en este artículo son consecuentes con la teoría modificada de la protección. El orden en las progresiones, claramente, no es al azar. Los machos adultos ocupaban la desguarnecida parte delantera de la progresión y en menor grado la trasera (fig. 2, tabla 1). Las hembras adultas y las jóvenes grandes se situaban en la parte trasera más a menudo que lo esperado (figs. 5, 6), mientras que los subadultos y los machos jóvenes grandes se encontraban más bien hacia adelante (figs. 6, 7). Esto permite que la zona central sea primariamente el dominio de los jóvenes menos experimentados y más vulnerables, es decir, las crías que pueden andar y los jóvenes más pequeños (figs. 3, 4). Los resultados se repiten en distintos grupos, especies, habitats y trabajos. La disposición de individuos en la progresión estaba asociada a los cambios en el desarrollo y al sexo de los individuos (tabla 2), basándose en procesos biológicos susceptibles de amoldarse a la evolución (RHINE et al., 1981; RHINE & WESTLUND, 1981). Las principales diferencias entre los resultados revisados aquí y las observaciones de Washburn y DeVore son que los machos dominantes estaban más bien en la parte delantera que en el centro y que las hembras que transportaban crías no se encontraban más en el centro del grupo que en otras zonas. Los aspectos más importantes de la teoría original — incluyendo la disposición no al azar, la naturaleza protectora del modelo socio-espacial de las progresiones y el origen adaptativo hipotético de la ordenación socio-espacial — se refiere a ambas versiones de la teoría, la original y la modificada. Los datos están de acuerdo con estos aspectos.

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