

## **Male Rank and Reproductive Activity in Savanna Baboons**

**Fred B. Bercovitch<sup>1</sup>**

*Received March 18, 1986; revised July 1, 1986*

---

*Access to sexually receptive baboon females has been linked to male dominance rank. An intensive 19-month field study of mate choice and mate competition among savanna baboons was undertaken in order to elucidate those factors influencing mating success. During this study, male agonistic rank was not correlated with male mating success among adult males. However, the inclusion of adolescent males into the analysis yielded significant correlations between rank and mating success. Examination of prior fieldwork revealed that no baboon field study has conclusively demonstrated a significant correlation between male rank and reproduction among adult males. Most studies reporting a correlation between male rank and reproduction have included subadult males in the analysis. It is concluded that male rank is an unreliable predictor of male reproductive activity among adult male baboons. A low agonistic rank need not reduce male mating success because adult male baboons utilize a variety of reproductive tactics in gaining access to consort females.*

---

**KEY WORDS:** savanna baboons; rank; reproduction; adult males.

### **INTRODUCTION**

A number of textbooks have claimed that dominant male baboons sire more offspring than lower-ranking males (Wittenberger, 1981; Stein and Rowe, 1982; Daly and Wilson, 1983; Alcock, 1984; McFarland, 1985; Nelson

<sup>1</sup>Wisconsin Regional Primate Research Center, University of Wisconsin, 1223 Capitol Court, Madison, Wisconsin 53715.

and Jurmain, 1985; Weiss and Mann, 1985; but see Richard, 1985). While this conclusion can be inferred from some field studies (Hausfater, 1975; Popp, 1978; Packer, 1979b; Rasmussen, 1980; Collins, 1981; Sapolsky, 1982), many other field studies of baboons have not revealed a significant correlation between male rank and male mating success (Hall, 1962; Hall and DeVore, 1965; Saayman, 1970, 1971; Harding, 1980; Ransom, 1981; Manzillo, 1982; Smuts, 1982; Strum, 1982; Scott, 1984). In addition, conflicting results have been reported from different studies of the same population. Packer (1979a, b) found a significant correlation between male rank and reproductive activity during his study of the baboons at the Gombe Stream Reserve, Tanzania, while Ransom (1981) found that male rank was not an accurate predictor of reproductive activity among the baboons at Gombe. The causes underlying these discrepant findings have yet to be determined.

One conspicuous factor that distinguishes reports linking male rank with reproductive activity from reports demonstrating no such association is the sampling procedure employed. Baboon field studies that have failed to uncover a correlation between male rank and mating activity have limited consideration to only adult males (e.g., Hall, 1962; Saayman, 1971; Harding, 1980; Smuts, 1982; Strum, 1982), while most of the baboon field studies that have reported a significant correlation between male rank and mating activity have included subadult males in their analysis (e.g., Hausfater, 1975; Popp, 1978; Packer, 1979a, b). One of the most frequently cited publications purporting to demonstrate a correlation between male rank and reproduction (Hausfater, 1975) included juvenile males in the analysis.

This report is an analysis of the influence of male rank on male reproductive activity among savanna baboons.<sup>2</sup> A 19-month field study of the baboons at Gilgil, Kenya was conducted in order to elucidate patterns of mate choice and mate competition. The results which emerged indicate that male rank is not correlated with male reproductive activity among adults. However, if subadult males are included in the analysis male rank does correlate with male reproductive activity. Although significant correlations between male rank and reproduction have been reported in the literature, reassessment of these reports supports the viewpoint that adult male rank is not a reliable predictor of male reproductive activity.

<sup>2</sup>Savanna baboons include yellow, olive, and chacma baboons. All three types are grouped together in this paper because their current taxonomic status indicates that they are either subspecies or races (Buettner-Janusch, 1966; Terry, 1977; Szalay and Delson, 1979; Shotake, 1981; Lucotte, 1983), and all three types share a number of common attributes in their reproductive activity (Collins, 1981; Bercovitch, 1985). The olive baboon troop observed in the present study has been considered *Papio anubis* but probably ought to be classified as *Papio hamadryas anubis* (Szalay and Delson, 1979) or *Papio cynocephalus anubis* (Terry, 1977).

## METHODS

### Subjects

In the Central African Rift Valley, adjacent to the town of Gilgil, Kenya, and 115 km northwest of Nairobi, one troop of olive baboons, Pumphouse Gang (PHG), has been the subject of nearly uninterrupted observations since 1970. The troop inhabits an environment of open grassland and patchy scrub punctuated by parallel outcroppings of volcanic cliffs (Harding, 1973, 1976).

The study reported here began on August 1, 1979, and terminated on March 1, 1981. Troop size varied from 78 to 90 baboons, including 4 to 8 adult males and 18 to 20 adult females. Focal sampling (Altmann, 1974) was confined primarily to adult individuals of both sexes. Female baboons were classified as adults following the birth of their first offspring (Strum and Western, 1982; Smuts, 1982). Male baboons were classified as adults when they were judged to be fully grown, as inferred from both canine eruption and the attainment of fully body size, which occurs between 8 and 10 years of age (Altmann *et al.*, 1981; Strum, 1982; Bercovitch, 1985). The use of body-size characteristics for determination of male adulthood is slightly subjective, but it is consistent across study sites (Rasmussen, 1980; Altmann *et al.*, 1981; Collins, 1981): The availability of morphological measurements obtained immediately prior to the commencement of this study (Byles *et al.*, 1980; Byles and Sanders, 1981; Sanders, 1981) aided in determining when males probably attained full body size. At 4 years of age, male baboons are classified as subadults.

During this study, 1980 hr of focal data was obtained from consortships and an additional 1167 hr of focal data was collected from nonconsort individuals. A consortship was defined as a continuous, close spatial association between a male and a sexually receptive female, with evidence of sexual activity by the male. The sampling regime is detailed by Bercovitch (1983, 1985) and is only summarized here.

Focal-subgroup samples (Altmann, 1974) were recorded from adult females and their consort partners. Sampling commenced between 0700 and 0800 and usually continued until 1700 to 1800, with a 1-hr lunch break during the day. Samples were obtained on consecutive days within a female's cycle from the initial day of consort commencement until the final day of consort dissolution. An assistant aided in data collection, which permitted observations to be collected on two focal subjects per day. If more than two females were in consort, sampling was restricted to the two females with the earliest anticipated cessation of consort activity, projected by inference from known characteristics of each female's menstrual cycling history (Bercovitch, 1985). If no females were in consort, observations were obtained from either

adult males or nonconsort, cycling adult females. Nonconsort focal samples were obtained by observing a single individual for 5 consecutive hr beginning between 0700 and 0800. Data recorded on an *ad libitum* basis (Altmann, 1974) were also included in the assessment of male rank.

Consortships formed during this study lasted for periods ranging from a few minutes to 1 week. Females averaged 5.1 cycles to conception and were in consort for an average of 5.6 days per cycle. More than two adult females formed consorts on 16.8% of the days when consortships occurred in the troop (Bercovitch, 1985).

### Assessment of Male Rank

The male dominance hierarchy was constructed based upon the system of least reversals in dyadic encounters combined with the number of males dominated (Rasmussen, 1980; Strum, 1982). Agonistic ranks were assigned to males on the basis of dyadic bouts involving either approach/avoidance interactions or supplants over resources other than consort females. These two types of interactions have been found to be the most reliable indicators of relative status (Rowell, 1966) and have been used in field studies of both rhesus macaques (Lindburg, 1971) and savanna baboons (Packer, 1979b; Rasmussen, 1980; Collins, 1981; Strum, 1982).

Interactions involving seizure of an infant by one of the participants were omitted from consideration, because the outcome of such interactions may depend upon which male is clutching the infant, rather than the relative status of the males (Popp, 1978; Packer, 1980; Strum, 1984). Only supplants over nonconsort female resources (e.g., food, water, location) or avoids of other male approaches were tallied. Access to female consorts was eliminated as a criterion of agonistic rank in order to assess the role of rank in obtaining sexually receptive females without using a circular definition of rank.

Criteria and techniques for assigning baboon male ranks are sometimes inconsistent between researchers. For example, Hausfater (1975) utilized the number of animals that an individual dominated based upon the expression of submissive gestures (e.g., avoiding eye contact, grimacing, moving away), while Packer (1979b) utilized the results of a computer simulation based upon supplants over resources because not enough interactions were observed to delineate a hierarchy on the basis of actual observations. A comparative assessment and evaluation of differing techniques for ranking individuals is beyond the scope of this report and has been considered elsewhere (Bernstein, 1981; Dewsbury, 1982; Strum, 1982; Fedigan, 1983).

The study period was partitioned into seven time blocks because of frequent changes in adult male membership. Time blocks were variable in length, with the boundaries determined by adult male migration and/or dissap-

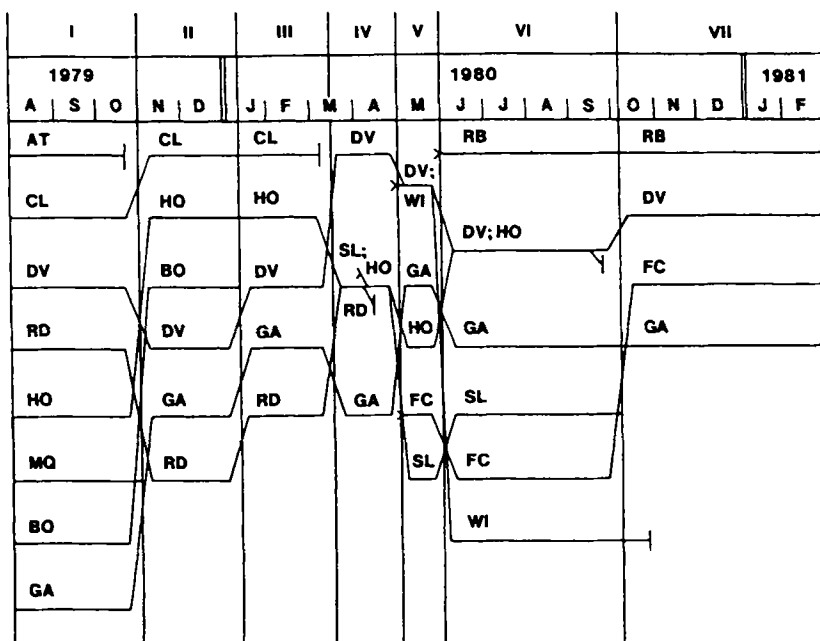


Fig. 1. Changes in male agonistic ranks based upon the outcome of dyadic encounters involving either approach/avoid interactions or supplants over resources other than consort females. Roman numerals at the top refer to the different time blocks.

pearance. A minimum period of 1 month per block was considered the smallest unit appropriate for analysis. Adult male agonistic ranks changed between time blocks (Fig. 1).

### Assessment of Male Reproductive Success

Various methods have been utilized to measure male reproductive success in polygamous mammals (Clutton-Brock *et al.*, 1982; Dewsbury, 1982; Fedigan, 1983; Bercovitch 1985, 1986). As was the case with assessing male rank, baboon field researchers have estimated male reproductive success with different criteria. For purposes of discussion, this report accepts the authors' assignment of both rank and reproductive success to males, although the criteria which have been utilized for measuring male reproductive success are questionable (Bercovitch, 1985, 1986).

The structure of baboon mating systems thwarts determination of paternity. The assumption made in most field studies is that the probability of insemination is associated with the proportion of ejaculations performed dur-

ing a female's most likely days of conception (Fedigan, 1983), but this assumption is long overdue for testing (Bercovitch, 1986). The term *mating success* is used in preference to the term *reproductive success* throughout this report.

Female baboons have enlarged sexual swellings in their anogenital region during the follicular stage of their cycle. The day of subsidence of the sex skin is considered to be cycle day 0, the last day of sexual swelling is -1, the day before that is -2, etc. (Hausfater, 1975). Conception almost always occurs between cycle day -7 and cycle day +1, but the greatest chance of conception is between day -3 and day 0 (Zuckerman, 1930; Gillman and Gilbert, 1946; Wildt *et al.*, 1977; Shaikh *et al.*, 1982; Pope *et al.*, 1983; Hodges *et al.*, 1986). Information available from endocrinology, laparotomy, embryo flushing, dissection, and pair testing suggests that the final 2 days of sexual swelling are the most probable days of conception (Bercovitch, 1985, in preparation).

Both Hausfater (1975) and Packer (1979a) suggested that high-ranking males achieve a higher mating success partly as a consequence of confining their reproductive activity to the most probable day of conception. Two different techniques have been used to measure cycle-day selectivity (CDS). Cycle-day selectivity refers to the confinement or concentration of male reproductive activity to the most probable ovulatory days within a cycle. Both of the measurements used to assess CDS omit consideration of synchronous cycles. Because the sampling schedule for this project was aimed at collecting data from those females who were predicted to be closer to the cessation of consort activity when more than two females consorted on the same day, a potential sampling bias may favor finding an association between rank and CDS. If males confined their consort activity to the most probable days of ovulation, the CDS values calculated may inflate their actual selectivity because of the sampling schedule.

In the first method, all males received a score based upon the proportion of available time that they spent in consort on cycle days -2 plus -1. Available time was determined by calculating the total amount of consort observation time for this 2-day period while the male was in PHG. In other words,

$$\text{CDS}(1) = \frac{\text{number of hours male consorted on } -2 \text{ plus } -1}{\text{number of consort observation hours on } -2 \text{ plus } -1 \text{ while male was in PHG}}$$

This measure addresses the question, did high-ranking males spend more time than other males in consort on the two most probable days of ovulation? It is essentially the same as Packer's (1979a) measure of consort activity, but it assesses the percentage of time in consort rather than the percentage

of female consort days. During this study, the time in consort was correlated with the percentage of female consort days during which a male was reproductively active (Bercovitch, 1986).

The second method ranks each male according to the proportion of his own consort time devoted to days  $-2$  plus  $-1$ . In other words,

$$\text{CDS}(2) = \frac{\text{number of hours a male consorted on } -2 \text{ plus } -1}{\text{number of hours a male consorted between } -7 \text{ and } +1}$$

This measure asks, in effect, did high-ranking males spend more of their own consort time than other males did with females on the two most probable days of ovulation? CDS(2) is essentially the same as the measure used by Hausfater (1975) to assess cycle-day selectivity, except that it considers the percentage of time rather than the percentage of copulations. During this study, a significant correlation existed between time in consort and ejaculatory success (Bercovitch, 1985, 1986).

All of the adult males in this study were ranked on both measures. These CDS rankings were then compared to male agonistic rankings. Because of fluctuations in the number and identity of males in the troop and in the ranks of males across time blocks, male agonistic rankings could not be assigned on a linear basis for the entire study period. Instead, males were assigned high, middle, or low ranks based upon their relative success in nonconsort agonistic interactions while they were in the troop.

## RESULTS

Table I presents the number of ejaculations accomplished by each adult male between cycle days  $-7$  and cycle day  $+1$ . In none of the seven time blocks was there a significant correlation between male agonistic rank and male mating success among adult males. Neither the proportion of ejaculations accomplished between day  $-7$  and day  $+1$  nor the proportion of ejaculations accomplished between day  $-3$  and day  $0$  correlated with male rank among adults (Table II). Across all time blocks, the average Spearman's correlation coefficient between male rank and male mating success among adults was nearly zero ( $r_s = -0.002$ ) when considering days  $-7$  to day  $+1$  and was virtually unchanged when considering cycle days  $-3$  to  $0$  ( $r_s = -0.009$ ). On the other hand, all seven time blocks yielded statistically significant correlations between male rank and male mating success when adolescent males were incorporated into the analysis (Table II). These results held for both cycle days  $-7$  to  $+1$  and cycle days  $-3$  to  $0$ .

**Table 1.** Number of Ejaculations by Each Male Within Each Time Block on Cycle Days -7 Through +1

Male	Ejaculations								
	-7	-6	-5	-4	-3	-2	-1	0	+1
<b>Time block I<sup>a</sup></b>									
AT	1	-	-	-	5	-	-	-	-
CL	-	-	-	-	-	1	-	-	-
DV	-	2	4	2	-	1	-	-	-
RD	-	-	-	-	-	-	-	-	-
HO	-	-	-	-	-	-	-	-	-
MQ	1	-	-	1	9	1	14	-	-
BO	-	-	-	-	-	-	-	-	-
GA	-	-	-	-	-	9	-	1	-
Sub <sup>b</sup>	-	-	-	-	1	-	-	-	-
<b>Time block II</b>									
CL	-	1	-	1	3	6	9	-	-
HO	-	3	5	-	10	10	6	11	-
BO	-	2	-	-	15	-	3	8	-
DV	-	2	5	7	-	15	2	2	-
GA	-	1	3	-	-	-	-	-	-
RD	-	-	-	-	-	-	-	-	-
Sub	-	2	-	-	-	-	-	5	-
<b>Time block III</b>									
CL	-	-	-	-	1	3	-	-	-
HO	-	-	-	-	1	2	4	-	-
DV	-	-	-	-	-	1	-	-	-
GA	-	-	-	-	1	3	13	1	-
RD	-	-	-	-	-	-	-	-	-
SL <sup>c</sup>	-	-	-	-	-	2	4	-	-
Sub	-	-	-	-	11	5	-	7	-
<b>Time block IV</b>									
DV	1	2	-	6	-	2	-	1	2
SL	4	11	11	9	12	11	5	8	-
RD	-	-	-	-	-	-	3	-	-
HO	11	12	18	9	11	-	-	8	-
GA	-	-	-	1	4	2	13	12	3
Sub	-	1	1	6	-	4	1	2	6
<b>Time block V</b>									
DV	-	3	-	-	-	6	-	6	3
WI	-	-	-	-	-	-	-	5	-
GA	-	-	3	3	6	-	4	8	-
HO	5	8	4	4	1	25	10	1	-
FC	-	-	-	-	-	-	-	-	-
SL	-	5	7	-	12	-	16	3	-
Sub <sup>c</sup>	-	-	-	-	4	-	-	-	-
<b>Time block VI</b>									
RB	5	4	2	17	14	20	20	-	-
DV	4	4	4	-	14	4	4	17	-
HO	5	7	3	13	6	19	10	5	-
GA	-	4	12	11	11	13	10	18	-
SL	10	7	-	4	28	26	44	14	-
FC	-	-	-	-	-	13	-	8	-
WI	-	-	-	-	2	3	7	7	-
Sub	-	-	2	4	-	-	5	1	-



Table I. Continued

Male	Ejaculations								
	-7	-6	-5	-4	-3	-2	-1	0	+1
Time block VII									
RB	—	—	—	16	15	10	12	14	—
DV	1	—	3	3	2	9	21	17	12
FC	—	—	—	—	11	36	32	38	15
GA	—	—	4	5	9	29	34	39	10
WI <sup>c</sup>	—	—	—	5	3	6	3	—	—
Sub	—	13	4	6	11	2	8	4	5

\*Males are listed in descending rank order within each time block. Agonistic ranks are based upon approach/avoid interactions.

<sup>b</sup>Subadult males.

<sup>c</sup>Male visited PHG and established at least one consortship but then returned to a neighboring troop.

Adult male rank was not associated with cycle-day selectivity during this study. Higher-ranking males did not confine their mating activity to days -2 plus -1 more than did lower-ranking males, nor did they appear to devote relatively more of their own consort time to these 2 days (Table III). Furthermore, the two measures of cycle day selectivity turned out to be discre-

Table II. Rank-Order Correlation Coefficients Between Male Agonistic Rank and Male Mating Success Within Each Time Block

Time block	Adult males	Adult and adolescent males
(A) Cycle days -7 through +1		
I	$r_s = -0.122, N = 8, ns^*$	$r_s = 0.537, N = 18, *$
II	$r_s = 0.600, N = 6, ns$	$r_s = 0.830, N = 16, ***$
III	$r_s = 0.300, N = 5, ns$	$r_s = 0.693, N = 15, **$
IV	$r_s = -0.224, N = 5, ns$	$r_s = 0.861, N = 17, ***$
V	$r_s = -0.290, N = 6, ns$	$r_s = 0.713, N = 19, ***$
VI	$r_s = 0.523, N = 7, ns$	$r_s = 0.928, N = 20, ***$
VII	$r_s = -0.800, N = 4, ns$	$r_s = 0.903, N = 18, ***$
	Average $r_s = -0.002,$	$r_s = 0.781$
(B) Cycle days -3 through 0		
I	$r_s = -0.061, N = 8, ns$	$r_s = 0.532, N = 18, *$
II	$r_s = 0.638, N = 6, ns$	$r_s = 0.705, N = 16, **$
III	$r_s = 0.300, N = 5, ns$	$r_s = 0.693, N = 15, **$
IV	$r_s = -0.574, N = 5, ns$	$r_s = 0.827, N = 17, ***$
V	$r_s = -0.290, N = 6, ns$	$r_s = 0.713, N = 19, ***$
VI	$r_s = 0.523, N = 7, ns$	$r_s = 0.879, N = 20, ***$
VII	$r_s = -0.600, N = 4, ns$	$r_s = 0.824, N = 18, ***$
	Average $r_s = -0.009$	Average $r_s = 0.739$

\*Nonsignificant ( $P > 0.05$ ).

\* $P < 0.05$ .

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

Table III. Cycle-Day Selectivity of Adult Males\*

	Male											
	AT	RD	BO	WI	RB	DV	FC	HO	CL	GA	SL	MQ
CDS(1)	0.0	3.6	3.8	5.4	11.1	11.5	12.4	19.4	24.7	26.8	28.2	61.6
Rank	12	11	10	9	8	7	6	5	4	3	2	1
CDS(2)	0.0	87.8	14.0	43.4	36.9	28.7	60.7	33.3	59.7	40.1	42.7	38.0
Rank	12	1	11	4	8	10	2	9	3	6	5	7
Status	H	L	M	M	H	H	L	M	H	M	L	L

\*CDS(1) measures the percentage of consort activity contributed by a male while in PHG during the 2 most likely days of conception (i.e., cycle days  $-2$  plus  $-1$ ); CDS(2) measures the percentage of each male's consort activity devoted to cycle days  $-2$  plus  $-1$ . The most selective male is awarded a rank of 1. Agonistic rank is based upon the average proportion of non-consort avoids and supplants across time blocks. H, high; M, middle; L, low ranking. See text for details.

pant with each other ( $r_s = 0.224$ ,  $N = 12$ ,  $P > 0.20$ ). The highest-ranking male on CDS(1), i.e., MQ, was low-ranking in agonistic interactions. The highest-ranking male on CDS(2), i.e., RD, consorted for less time than any other adult male. He was in consort for less than 10 hr during the entire study. Of the two males who had the highest agonistic ranks while in the troop, i.e., AT and RB (see Fig. 1), one scored lowest on both CDS scores.

These results remained consistent within each of the seven time blocks (Table IV). In none of the time blocks was male rank significantly correlated with the proportion of ejaculations contributed on the two most probable days of conception. In fact, although the correlations were nonsignificant, four time blocks yielded negative associations between the two measures. The average Spearman's correlation coefficient between adult male rank and percentage of ejaculations accomplished on cycle days  $-2$  plus  $-1$  was essentially zero ( $r_s = -0.075$ ).

Some field-workers (Hausfater, 1975; Seyfarth, 1978a; Packer, 1979a, b; Collins, 1981; Scott, 1984) have assumed that cycle day  $-3$  is the most likely day of conception in savanna baboons, but as noted earlier, the best available information implicates cycle day  $-2$  or  $-1$  as the most probable day of fertilization. Examination of mating patterns on day  $-3$  using the current data set is essentially a moot analysis, but the following analysis was performed in order to incorporate the data obtained from this study into the earlier framework for comparative purposes.

Agonistic ranks of adult males were compared with their mating success on day  $-3$  for each of the seven time blocks. In none of the time blocks was there a significant correlation between agonistic rank and mating success on cycle day  $-3$ . The average Spearman's correlation coefficient for all time blocks was 0.164 during this study. Hence, high-ranking males in this study did not concentrate their reproductive activity upon cycle day  $-3$ .

**Table IV.** Spearman's Rank-Order Correlations Between CDS(1) and Male Agonistic Rank for the Seven Time Blocks

Time block I:	$r_s = -0.332, N = 8, ns^*$
Time block II:	$r_s = 0.580, N = 6, ns$
Time block III:	$r_s = 0.300, N = 5, ns$
Time block IV:	$r_s = -0.300, N = 5, ns$
Time block V:	$r_s = -0.271, N = 6, ns$
Time block VI:	$r_s = 0.295, N = 7, ns$
Time block VII:	$r_s = -0.800, N = 4, ns$
Average $r_s = -0.075$	

\*Nonsignificant.

In sum, male agonistic rank was correlated with male mating success only when adolescent males were included in the analysis. Among adult males, rank did not correlate with reproductive activity. High-ranking males did not spend relatively more of their own time, or more time than low-ranking males, with sexually receptive females on the most probable days of conception in savanna baboons.

## DISCUSSION

The results from this study concur with other reports which have emerged from the Gilgil Baboon Project. Observations conducted over a 10-year period at Gilgil, Kenya, have consistently failed to find a positive correlation between baboon male rank and male mating activity (Harding, 1980; Manzollilo, 1982; Smuts, 1982; Strum, 1982; Scott, 1984). The present study was initiated shortly after the cessation of a 3-year study on the same troop by Manzollilo (1982). She divided her study period into nine time blocks and found no significant correlation between male agonistic rank and consort success in any time block. The average Spearman's correlation coefficient across all time blocks during her study was 0.087 (calculated from Table 19 of Manzollilo, 1982). Given the long-term observations at this site, coupled with the consistency in results, the finding that male reproductive activity is not correlated with male rank at Gilgil seems quite robust. This lack of a correlation between male rank and reproductive activity runs counter to the pattern which is generally assumed, yet it has been reconfirmed by independent investigations.

This study supports Dewsbury's (1982) suggestion that some anomalies in the literature on male rank and reproduction can be explained because some researchers included immature males in their analysis. A significant correlation between baboon male rank and mating success occurred during

this study only when subadult males were incorporated into the analysis. It has been reasoned that because juvenile males are capable of producing viable sperm, and are thus potential sires, they ought to be included in assessing the influence of male rank on reproduction (Hausfater, 1975). During this study, the youngest male observed to ejaculate with a sexually swollen adult female was 4 years old. The youngest male observed maintaining a consortship for at least 1 hr with an adult female between cycle day - 3 and cycle day 0 was 6.5 to 7 years old. Immature males contributed less than 6% of the ejaculations during the 4 most likely days of conception. Hence, males can probably produce viable sperm before they are fully capable of controlling lengthy access to sexually receptive baboon females, and a proper understanding of the role of male rank in influencing male reproduction would exclude immature males.

Field studies of both rhesus macaques (*Macaca mulatta*) (McMillan, 1982) and Japanese macaques (*M. fuscata*) (Takahata, 1982) have also revealed that a significant correlation between male rank and male mating activity becomes nonsignificant when subadult males are excluded from the analysis. In these studies, male rank was not correlated with male mating activity among adults. Since subadult male baboons generally have lower mating success than adult male baboons, as well as lower agonistic ranks, the inferred correlations in many studies (e.g., Hausfater, 1975; Popp, 1978; Packer, 1979a, b) may be a consequence of the failure to omit subadult males from the analysis. Unfortunately, the published data in these studies are inadequate to permit a reanalysis based exclusively on adult males.

Elements other than the inclusion of immature males can also explain positive correlations between male rank and reproduction. If the highest- and lowest-ranking males in Rasmussen's (1980) study are excluded from the analysis, one finds no positive correlation between rank and mating activity among the remaining eleven adult males. Hence, her reported correlation is entirely attributable to the behavior of two extreme outliers. Cheney (1978) noted that male rank was associated with mating activity in her study troop in South Africa, but that troop contained only two adult males and eight adult females, and Seyfarth (1978b) has cautioned against extending the results of that study to larger multimale troops.

Perhaps the most peculiar situation concerns DeVore's work (DeVore, 1965; Hall and DeVore, 1965). His study is frequently cited as demonstrating that male rank is correlated with male mating success, yet no claim for such a relationship can be found in the report. He found that the lowest-ranking adult male had the second highest mating success and that a linear dominance hierarchy did not characterize the primary study troop. Using DeVore's data to construct a male hierarchy according to relative success on food incentive tests, one finds no statistically significant correlation between male rank and

the proportion of completed copulations at full estrus ( $r_s = 0.152$ ,  $N = 6$ ,  $P > 0.50$ ). In other studies, the highest-ranking adult male baboon has often proved not to have the highest mating success (Hausfater, 1975; Strum, 1982; Sapolsky, 1983; Bercovitch, 1985).

In summary, field studies of savanna baboons have not provided adequate evidence for concluding that male rank is correlated with male reproductive activity among adult males. However, a nonsignificant pattern does not preclude a positive relationship between male rank and reproduction if higher-ranking males are selectively mating with sexually receptive females near the optimum time of ovulation.

The data which emerged from this study did not suggest that males were partitioning their consort activity across female cycle days with respect to male rank. All of the adult males tended to confine their consort activity to cycle days  $-3$  to  $0$  (Bercovitch, 1985). A careful scrutiny of the published data from other study sites leads to the same conclusion.

Rasmussen (1980) found that higher-ranking males consorted more often between day  $-4$  and day  $-1$  than did lower-ranking males but that higher-ranking males did not restrict their consort activity to this period more than did lower-ranking males. Smuts (1982) postulated that cycle-day selectivity corresponded with male rank based upon her calculation of a "weighted" consort success score for days  $-7$  through  $-2$ . Her weighted measure of consort success, however, excludes one of the most probable days of conception while including quite a few days with minimal chances of conception. The probabilities that she used for deriving a weighted score are no longer regarded as accurate indicators of the chances of fertilization (Bercovitch, 1985).

Hausfater (1975) found that high-ranking males performed a greater proportion of their *own* copulations on day  $-3$  than did other males. But this could occur if males were rarely in consort, as in RD's case, mentioned above. During Hausfater's study, third-ranking males accomplished 2.5 times as many ejaculations during days  $-2$  plus  $-1$  as did first-ranking males. Reanalysis of Hausfater's data (1975, Table XXIX), using CDS(1) and limiting the analysis to those males who ejaculated at least once on either cycle day  $-2$  or cycle day  $-1$  reveals no statistically significant correlation between male rank and the proportion of ejaculations accomplished on the 2 most probable days of conception ( $r_s = 0.506$ ,  $N = 10$ ,  $P > 0.10$ ).

Packer (1979a) deduced cycle-day selectivity from the performance of the highest-ranking males in each of four different troops. All four males tended to concentrate their mating activity on day  $-3$ . However, none of the four males had a single unique day of maximal consort activity. The consort activity scores were identical for days  $-3$  and  $-2$  in three males and for days  $-3$  and  $-1$  in the fourth male (Packer 1979a, Table XII). While

these results imply that the highest-ranking male in a troop was relatively selective, data were not reported on the selectivity of subalpha males. It seems likely that all adult males were concentrating their reproductive activity on the few days preceding deturgescence, as has been reported from other field sites (DeVore, 1965; Hausfater, 1975; Rasmussen, 1980; Collins, 1981; Bercovitch, 1985). The cycle-day selectivity deduced by Packer was not confined to a single day and is not necessarily a trait limited to high-ranking males.

Neither the observations emerging from this study nor the data reported by others persuasively demonstrate that high-ranking males are more selective about which cycle days they consort on than are low-ranking males. All studies do concur in demonstrating that male interest in cycling females peaks when females are maximally swollen. Rather than male rank being associated with cycle-day selectivity, all adult males tend to concentrate their consort behavior upon the most likely days of conception.

Contrary to the common conclusion presented in the literature, savanna baboon male rank is probably not correlated with reproductive activity. To date, not a single field study of savanna baboons has *conclusively* demonstrated a *significant* correlation between male rank and male mating success among *adult* males. On occasion, male rank may influence access to consort females, but in general, adult male rank in baboons is an unreliable predictor of male mating activity or of cycle-day selectivity.

Male agonistic ranks may not be associated with male mating success for two primary reasons. First, male baboons maintain an unstable, shifting hierarchical relationship with each other (Hall and DeVore, 1965; Hausfater, 1975; Packer, 1979b; Manzollillo, 1982; Strum, 1982; Bercovitch, 1985). Such a dominance structure would militate against detecting a close correlation between male rank and reproduction. With males frequently altering their status relative to one another, it would not be expected that an assertion of rank by a male would necessarily enable that male to obtain a contested resource. Second, male baboons utilize a variety of reproductive tactics to gain access to sexually receptive females (Packer, 1979b; Strum, 1982; Bercovitch, 1985), and the use of these tactics can overcome the potential influence of male agonistic rank. The use of complex social strategies in adjudicating conflicts between individuals within a primate social group seems to be a major factor which underlies much of primate social behavior (Strum, 1982; de Waal, 1982; Western and Strum, 1983; Bercovitch, 1985). Male chimpanzees (*Pan troglodytes*) adopt a diverse array of reproductive tactics for gaining access to sexually receptive females (Tutin, 1979; Tutin and McGinnis, 1981; Hasegawa and Hiraiwa-Hasegawa, 1983), and male rank is an unreliable predictor of male mating success (Tutin, 1979; Hasegawa and Hiraiwa-Hasegawa, 1983).

If complex social strategies operate to influence mate competition between adult males, one may make the following prediction: among primate

species where males utilize a diversity of mating tactics, one is less likely to find a significant correlation between male rank and male mating success than among primate species where males adopt fewer mating tactics.

In conclusion, male rank is a negligible factor influencing access to consort female baboons. Adult male mating success is not predictable on the basis of male rank or male weight (Packer, 1979b; Smuts, 1982; Bercovitch, 1985). In order to understand the mating system of savanna baboons, it seems important to shift the focus of attention away from simple male attributes and toward the complex social strategies that males use for gaining access to sexually receptive females. The key to differences in male reproductive success probably lies outside the realm of relative male dominance status.

### ACKNOWLEDGMENTS

Permission to conduct research in Kenya was granted by the Office of the President of the Republic of Kenya. Local sponsorship and help were provided by Jim Else. We appreciated all of the household services performed by Samuelli Azango Didi. Bob Harding and Shirley Strum allowed us to observe PHG, and Richard Dansie granted permission to reside on Kekopey Ranch. This paper is based upon a doctoral dissertation which was read by Dorothy Cheney, Don Lindburg, Mike McGuire, Shirley Strum, and B. J. Williams. The paper has benefited substantially from the suggestions of two reviewers. Research funds were provided by NIMH Grant 5T32MH15133. Computer funds were supplied by the Office of Academic Computing (UCLA) and a grant from the Chancellor's Patent Fund. Current support is provided by NIH Grant 5T32HD07118, with additional funding made available through NIH Grant RR00167 to the Wisconsin Regional Primate Research Center. This is publication No. 26-020 of the WRPRC.

### REFERENCES

- Alcock, J. (1984). *Animal Behavior*, Sinauer Associates, Sunderland, Mass.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227-267.
- Altmann, J., Altmann, S., and Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *Am. J. Primatol.* 1: 389-399.
- Bercovitch, F. B. (1983). Time budgets and consortships in olive baboons (*Papio anubis*). *Folia primatol.* 41: 180-190.
- Bercovitch, F. B. (1985). *Reproductive Tactics in Adult Female and Adult Male Olive Baboons*, Ph.D. dissertation, University of California at Los Angeles.
- Bercovitch, F. B. (1986). Measurements of male baboon mating success (submitted for publication).
- Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behav. Brain Sci.* 4: 419-457.

- Buettner-Janusch, J. (1966). A problem in evolutionary systematics: Nomenclature and classification of baboons, genus *Papio*. *Folia primatol.* 4: 288-308.
- Byles, R. H., and Sanders, M. F. (1981). Intertroop variation in the frequencies of ABO alleles in a population of olive baboons. *Int. J. Primatol.* 2: 35-46.
- Byles, R. H., Sanders, M. F., Petersen, G. M., Olivier, T. J., Bercovitch, F. B., and Hunt, E. (1980). A-B-O blood groups in Kenya olive baboons (*Papio anubis*). *Anim. Blood Grps. Biochem. Genet.* 11: 245-249.
- Cheney, D. L. (1978). Interactions of immature male and female baboons with adult females. *Anim. Behav.* 26: 389-408.
- Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- Collins, D. A. (1981). *Social Behaviour and Patterns of Mating Among Adult Yellow Baboons* (*Papio c. cynocephalus L. 1776*), Ph.D. dissertation, University of Edinburgh, Edinburgh.
- Daly, M., and Wilson, M. (1983). *Sex, Evolution, and Behavior*, Willard Grant Press, Boston.
- Dewsbury, D. A. (1982). Dominance rank, copulatory behavior, and differential reproduction. *Q. Rev. Biol.* 57: 135-159.
- DeVore, I. (1965). Male dominance and mating behavior in baboons. In Beach, F. A. (ed.), *Sex and Behavior*, John Wiley and Sons, New York, pp. 266-289.
- de Waal, F. (1982). *Chimpanzee Politics*, Harper and Row, New York.
- Fedigan, L. M. (1983). Dominance and reproductive success in primates. *Yb. Phys. Anthropol.* 26: 91-129.
- Gillman, J., and Gilbert, C. (1946). The reproductive cycle of the chacma baboon (*Papio ursinus*) with special reference to the problems of menstrual irregularities as assessed by the behaviour of the sex skin. *S. Af. J. med. Sci. (Suppl.)* 11: 1-54.
- Hall, K. R. L. (1962). The sexual, agonistic and derived social behaviour patterns of the wild chacma baboon, *Papio ursinus*. *Proc. zool. Soc. London* 139: 283-327.
- Hall, K. R. L., and DeVore, I. (1965). Baboon social behavior. In DeVore, I. (ed.), *Primate Behavior*, Holt, Rinehart and Winston, New York, pp. 53-110.
- Harding, R. S. O. (1973). *Range Utilization by a Troop of Olive Baboons* (*Papio anubis*), Ph.D. dissertation, University of California at Berkeley.
- Harding, R. S. O. (1976). Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. *Folia primatol.* 25: 143-185.
- Harding, R. S. O. (1980). Agonism, ranking, and the social behavior of adult male baboons. *Am. J. phys. Anthropol.* 53: 203-216.
- Hasegawa, T., and Hiraiwa-Hasegawa, M. (1983). Opportunistic and restrictive matings among wild chimpanzees in the Mahale Mountains, Tanzania. *J. Ethol.* 1: 75-85.
- Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). *Contrib. Primatol.* 7: 1-150.
- Hodges, J. K., Tarara, R., Hearn, J. P., and Else, J. G. (1986). The detection of ovulation and early pregnancy in the baboon by direct measurement of conjugated steroids in urine. *Am. J. Primatol.* 10: 329-338.
- Lindburg, D. G. (1971). The rhesus monkey in North India: an ecological and behavioral study. In Rosenblum, L. A. (ed.), *Primate Behavior*, Academic Press, New York, Vol. 2, pp. 1-106.
- Lucotte, G. (1983). Bases génétiques de la spéciation et de la taxonomie chez les babouins. *Biochem. Syst. Ecol.* 11: 145-158.
- McFarland, D. (1985). *Animal Behaviour*, Benajmin/Cummings, Menlo Park, Calif.
- McMillan, C. A. (1982). Male age and mating success among rhesus macaques. *Int. J. Primatol.* 3: 312.
- Manzollilo, D. L. (1982). *Intertroop Transfer by Adult Male Papio anubis*, Ph.D. dissertation, University of California at Los Angeles.
- Nelson, H., and Jurmain, R. (1985). *Introduction to Physical Anthropology*, West, St. Paul, Minn.
- Packer, C. (1979a). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* 27: 1-36.



- Packer, C. (1979b). Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.* 27: 37-45.
- Packer, C. (1980). Male care and exploitation of infants in *Papio anubis*. *Anim. Behav.* 28: 512-520.
- Pope, V. Z., Pope, C. E., and Beck, L. R. (1983). A 4-year summary of the nonsurgical recovery of baboon embryos: A report on 498 eggs. *Am. J. Primatol.* 5: 357-364.
- Popp, J. L. (1978). *Male Baboons and Evolutionary Principles*, Ph.D. dissertation, Harvard University, Cambridge, Mass.
- Ransom, T. W. (1981). *Beach Troop of the Gombe*, Bucknell University Press, Lewisburg, Pa.
- Rasmussen, K. L. R. (1980). *Consort Behaviour and Mate Selection in Yellow Baboons* (*Papio cynocephalus*), Ph. D. dissertation, Cambridge University, Cambridge.
- Richard, A. F. (1985). *Primates in Nature*, W. H. Freeman, New York.
- Rowell, T. E. (1966). Hierarchy in the organization of a captive baboon group. *Anim. Behav.* 14: 430-443.
- Saayman, G. S. (1970). The menstrual cycle and sexual behaviour in a troop of free ranging chacma baboons. *Folia primatol.* 12: 81-110.
- Saayman, G. S. (1971). Behaviour of the adult males in a troop of free-ranging chacma baboons (*Papio ursinus*). *Folia primatol.* 15: 36-57.
- Sanders, M. F. (1981). *Genetic Microdifferentiation and Evolution in a Population of Kenyan Olive Baboons* (*Papio anubis*), Ph.D. dissertation, University of California at Los Angeles.
- Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Horm. Behav.* 16: 279-292.
- Sapolsky, R. M. (1983). Endocrine aspects of social instability in the olive baboon (*Papio anubis*). *Am. J. Primatol.* 5: 365-379.
- Scott, L. M. (1984). Reproductive behavior of adolescent female baboons (*Papio anubis*) in Kenya. In Small, M. F. (ed.), *Female Primates: Studies by Women Primatologists*, Alan R. Liss, New York, pp. 77-100.
- Seyfarth, R. M. (1978a). Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. *Behaviour* 64: 204-226.
- Seyfarth, R. M. (1978b). Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. *Behaviour* 64: 227-247.
- Shaikh, A. A., Celaya, C. L., Gomez, I., and Shaikh, S. A. (1982). Temporal relationship of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates* 23: 444-452.
- Shotake, T. (1981). Population genetical study of natural hybridization between *Papio anubis* and *P. hamadryas*. *Primates* 22: 285-308.
- Smuts, B. (1982). *Special Relationships between Adult Male and Female Olive Baboons* (*Papio anubis*), Ph.D. dissertation, Stanford University, Stanford, Calif.
- Stein, P. L., and Rowe, B. M. (1982). *Physical Anthropology*, McGraw-Hill, New York.
- Strum, S. C. (1982). Agonistic dominance in male baboons: An alternative view. *Int. J. Primatol.* 3: 175-202.
- Strum, S. C. (1984). Why males use infants. In Taub, D. M. (ed.), *Primate Paternalism*, Van Nostrand Reinhold, New York, pp. 146-185.
- Strum, S. C., and Western, J. D. (1982). Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *Am. J. Primatol.* 3: 61-76.
- Szalay, F. S., and Delson, E. (1979). *Evolutionary History of the Primates*. Academic Press, New York.
- Takahata, Y. (1982). The socio-sexual behaviour of Japanese monkeys. *Z. Tierpsychol.* 59: 89-108.
- Terry, M. W. (1977). Use of common and scientific nomenclature to designate laboratory primates. In Schrier, A. M. (ed.), *Behavioral Primatology*, Lawrence Erlbaum Associates, New York, Vol. 1, pp. 1-32.
- Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 6: 29-38.

- Tutin, C. E. G., and McGinnis, P. R. (1981). Chimpanzee reproduction in the wild. In Graham, C. E. (ed.), *Reproductive Biology of the Great Apes*, Academic Press, New York, pp. 239-264.
- Weiss, M. L., and Mann, A. E. (1985). *Human Biology and Behavior*, Little, Brown, Boston.
- Western, J. D., and Strum, S. C. (1983). Sex, kinship and the evolution of social manipulation. *Ethol. Sociobiol.* 4: 19-28.
- Wildt, D. E., Doyle, L. L., Stone, S. C., and Harrison, R. M. (1977). Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and the ovarian follicular development during the baboon reproductive cycle. *Primates* 18: 261-270.
- Wittenberger, J. F. (1981). *Animal Social Behavior*, Duxbury Press, Boston.
- Zuckerman, S. (1930). The menstrual cycle of the primates. Part I. General nature and homology. *Proc. zool. Soc. London* 1930: 691-754.