American Journal of Primatology 55:117–130 (2001)

Analysis of Infant Handling and the Effects of Female Rank Among Tana River Adult Female Yellow Baboons (*Papio Cynocephalus Cynocephalus*) Using Permutation/ Randomization Tests

VICKI K. BENTLEY-CONDIT[1*], THOMAS MOORE[2], AND E.O. SMITH[3]
[1] *Department of Anthropology, Grinnell College, Grinnell, Iowa*
[2] *Department of Mathematics and Computer Science, Grinnell College, Grinnell, Iowa*
[3] *Department of Anthropology, Emory University, Atlanta, Georgia*

Infant handling has been documented in numerous species. Among cercopithecines, interaction motivations are reported to range from aunting to kidnapping; these interactions are often distressful for both mother and infant. Here we examine handling by adult female yellow baboons (*Papio cynocephalus cynocephalus*) at the Tana River National Primate Reserve, Kenya, using a relatively new, computer-intensive statistical approach of permutation/randomization tests to deal with repeated measures effects and a skewed sample. We hypothesized 1) a tendency for handlers to handle the infants of females ranked similarly or lower than themselves, and 2) more successful infant handling by higher-ranked females, particularly with very young infants. We collected focal data on 23 females (11 mother–infant pairs) over an 11-mo period, with a total of 303 attempted and/or successful "handles" utilized in the permutation analyses. The general patterns apparent in the data seemed to support our hypotheses. However, the permutation tests showed that while females are somewhat more likely to attempt to handle the infants of females ranked "same or lower" than themselves, lower-ranked females are able to prevent more than three-fourths of the attempted interactions, and there is no statistically significant trend for females to successfully handle these infants. Further refinement of the analyses showed no significant tendencies for females to handle those infants ranked "lower" or "immediately lower" than themselves, casting doubt on the significant finding for "same or lower" attempts. Further, there was no significant effect for higher-ranked females to successfully handle an infant during its first month. Thus, rank does not seem to offer any privileges in terms of handling an infant in this population. We believe the permutation tests are an effective way to analyze repeated measures data and offer a more sensitive analysis tool for determining true significance. Am. J. Primatol. 55:117–130, 2001. © 2001 Wiley-Liss, Inc.

Contract grant sponsor: L.S.B. Leakey Foundation; Contract grant sponsor: Mellon Foundation; Contract grant sponsor: Sigma Xi; Contract grant sponsor: NSF; Contract grant number: BNS-8921106; Contract grant sponsor: Emory University Research Committee; Contract grant sponsor: NIH; Contract grant number: RR-00165.

*Correspondence to: Vicki K. Bentley-Condit, Ph.D., Department of Anthropology, Grinnell College, Grinnell, IA 50112. E-mail: bentleyc@grinnell.edu

Received 16 January 1999; revision accepted 26 June 2001

Key words: ***Papio cynocephalus*; baboons; infant handling; dominance; permutation tests**

INTRODUCTION

It is common knowledge among primatologists that adult female primates interact with the infants of other females. While a complete review of the literature is beyond the scope of this manuscript, even a cursory review reveals a large body of data, spanning more than four decades, describing these interactions in detail. These female–infant interactions have been labeled variously as aunting [Rowell et al., 1964; Hrdy, 1976], babysitting [Hunt et al., 1978], playmothering [Lancaster, 1971], allomothering [Hrdy, 1978; Small, 1990], kidnapping [Bullerman, 1950; Strum, 1987; Nakagawa, 1995], and, more recently (and at the urging of Wasser and Barash [1981]) are often labeled using the more neutral term of infant handling [Maestripieri, 1994; Manson, 1999; Paul, 1999]. Following the lead set by these last researchers, we, too, will use this neutral infant-handling terminology. All of the researchers cited above have shown, as well, that there is considerable intra- and interspecific variation in the expression of infant handling.

It is easy to see why there should be a close relationship between a mother and her own offspring because of the obvious fitness-enhancing possibilities for both. The underlying basis for nonmother–infant (i.e., female–infant) associations and infant-handling behavior is less obvious. Several hypotheses have been advanced to explain the function and evolution of these behaviors (e.g., inclusive fitness [Hamilton, 1964], learning to mother [Lancaster, 1971], and selective infanticide [Mohnot, 1980]. Though these hypotheses, too, are beyond the scope of this study, they are reviewed and summarized in an excellent paper by Maestripieri [1994]. Infant-handling interactions are situated in a social milieu of dominance relationships, friends, allies, kin, and competitors. Any interaction with an unweaned infant must involve that infant's mother due to the very nature of the mother–infant bond and the period of infant dependency. The result is a mother–infant–handler triad which may have potentially long and far-reaching effects for all involved individuals and which warrants closer examination. These interactions are not isolated events; they represent another link in the females' and the infants' social networks. Thus, the infant-handling interaction presents a complex situation that may be best understood when examined in relation to other social associations.

There are some excellent recent accounts of infant handling among other Old World monkeys (e.g., Barbary macaques [Paul, 1999] and New World monkeys (e.g., white-faced capuchins [Manson, 1999] and exceptional cross-species comparisons by other researchers [Mitani & Watts, 1997; Paul, 1999]. However, baboon species' infant handling interactions are less studied phenomena. Most descriptions and discussions of baboon infant handling have been ancillary to other topics, such as mothers and infants [Altmann, 1980], males and females [Smuts, 1985], or issues such as infanticide [Collins et al., 1984]. Infant handling is, however, an important topic given the potential impact of these interactions upon the mother, the infant, and possibly the handling female. We examine these infant-handling interactions and, in particular, the impact of mothers' and handlers' ranks in a relatively unstudied population of yellow baboons.

Our goal in the collection of these data was to examine the influence of established female relationships via female rank on the patterns and successes (i.e, completed vs. attempted interactions) of infant-handling interactions within this population. Based primarily upon data published from the well-studied population of yellow baboons at Amboseli [Altmann, 1980], and upon other studies addressing the privileges of high rank among savanna baboon females [Altmann et al., 1988; Barton, 1993], one would expect female rank to affect a female's ability to handle (or to prevent the handling of) an infant. Thus, we proposed the following hypotheses:

1. If rank is an important factor influencing infant-handling interactions, females should primarily handle the infants of females ranked similar to, or lower than, themselves (i.e., same or lower) rather than those of females ranked higher than themselves.
2. If rank is important, higher-ranked females should be more successful in obtaining access to and handling infants than their lower-ranked conspecifics—particularly the highly sought, very attractive, youngest infants.

These hypotheses were tested through statistical analyses of the infant-handling data via permutation tests and incorporation of previously published data [Bentley-Condit & Smith, 1999] on the Tana River yellow baboon (Mchelelo Troop) females' dominance ranks.

METHODS

The data presented are based on observations of the Mchelelo yellow baboon troop in the Tana River National Primate Reserve (TRNPR), Kenya. The TRNPR is located in eastern Kenya at 1°55′S, 40°5′E and consists of approximately 171 km^2 of land bisected by the Tana River. (See Condit and Smith [1994] for a more detailed discussion of the study site and a map.)

Included in the Mchelelo study were 23 (of a possible 25) focal females, 11 of whom had infants. The two females excluded from the study had older, "brown" infants. The infants included ranged in age from newborn to 1 year over the course of the study. The data are thus both longitudinal and cross-sectional. Twenty-minute focal samples [Altmann, 1974] were collected on these females and mother–infant pairs over an 11-mo period in 1991–1992 for a total of 600+ hr of focal observations. The reader is referred to Bentley-Condit and Smith (1999] for a more detailed description of study methodology and dominance hierarchy determinations. However, as the dominance hierarchy is an integral component of this infant-handling discussion and the methods of analysis, an abbreviated presentation of the dominance methodology follows below.

The females' dominance hierarchy was calculated based upon both aggressive and submissive behaviors. Following Bramblett [1981], in each dyad a given female received a "+1" if dominant, a "–1" if submissive, and a "0" if no determination could be made. Each of the focal females were then assigned a score based upon net individuals (all) to whom they were dominant. Thus, for 23 focal females, scores could range from +22 to –22. The rankings formed themselves into three logical groupings of High Rank (n = 4♀), Mid Rank (n = 7♀), and Low Rank (n = 12♀). These categories and the number of females in each are utilized in the permutation tests described later in this section.

Having previously determined the dominance hierarchy, we categorized the infant-handling data as either: 1) movement to within 1 m of the mother–infant pair, with an attempted but unsuccessful handle (i.e., an attempt); or 2) movement to within 1 m of the mother–infant pair, with a successful handle (i.e, a success).

In an attempted handling interaction, the "handler" female achieved contact with the infant but was unable to transfer the infant. In a successful handling interaction, the "handler" female was able to transfer the infant. These categorizations are similar to Altmann's [1980] classifications of interactive and noninteractive. Because we were interested in infant handling rather than other categories of contact interactions with infants (e.g., grooming), we limit our discussion to those interactions in which a *transfer* was attempted and/or completed. We also incorporate an analysis of the effects of infant age by focusing on two categories (i.e., ≤ 1 mo of age and > 1 mo of age). We were particularly interested in the very young infants, and several studies have shown that mothers restrict access to their infants most vehemently during the first month (e.g., olive baboons [Nicolson, 1982] and Japanese macaques [Hiraiwa, 1981]).

All of the infant-handling episodes tended to be brief; therefore, our analyses rely on frequencies of occurrence rather than durations. Because it is the focal female who endeavors to transfer the infant and who initiates the interactions, the data are presented and analyzed from her point of view rather than the infant's.

Statistical Inference for the Research Hypotheses

The observational, as opposed to experimental, nature of our data complicates the data analyses in several ways. First, we could not control for such factors as the number of infants available or number of females in each ranking category; such control would have permitted a more balanced data set and thus greater power in any statistical tests. Second, the subjects (handlers and mothers) are not randomly assigned ranks (as they would be in a true experiment). Ranks are inextricably tied to the individual personalities of females, and the application of significance tests carries the caveat associated with any application of statistical inference to observational data: conclusions are correlational, not causal.

Finally, the most venerable of categorical significance tests, the chi-square test of independence, will not work with our data. A chi-square test would require that our interactions be independent of one another—a requirement that our data fail to meet, as the interactions presented in the Results section (see Tables I and II) are "repeated measures" for each handler–infant pair. Since the frequencies of interaction cluster themselves in complicated ways throughout the data set, a significance test must account for this clustering or repeated measures effect. We thus use permutation (i.e., randomization) tests to test our relationships. "Permutation tests are a computer-intensive statistical technique that predates computers. The idea was introduced by R.A. Fisher in the 1930's, more as a theoretical argument supporting Student's t-test than as a useful statistical technique in its own right. Modern computational power makes permutation tests practical to use on a routine basis. The basic idea is attractively simple and free of mathematical assumptions" [Efron & Tibshirani, 1998, p. 200]. Because this methodology is still rather new to primatology, we provide a relatively detailed description below. (The reader is also referred to Moore and Bentley-Condit [2001] for further examples of the permutation test computation process.)

Randomization/Permutation Tests

While randomization/permutation tests are not yet routine in primatological and anthropological studies, they are beginning to find their way into the litera-

TABLE I. Infant Approach/Attempted/Successful Handling Frequency Matrix*

Rank		High			Mid					Low				
Female		KM	HQ	LL	NY	PS	CO	LS	ML	MH	MM	PH		
		(n=1)		(n=4)		Infant			(n=6)				Female totals	Rank total
		KG	HZ	LC	NK	PZ	CY	LZ	MQ	MW	MX	PK		
High (n=4)	KM	XX	2/4/7	0/2/2	5/5/2	0/0/1	0/2/0	1/0/0	0/0/0	0/3/0	0/2/0	1/1/0	40	
	KN	0/0/0	8/10/5	0/0/0	4/0/0	2/0/1	1/1/0	0/0/0	1/0/0	0/0/0	3/0/0	0/0/0	36	
	NQ	4/0/0	4/3/0	1/0/0	6/4/0	3/1/0	4/3/0	1/2/0	5/0/0	6/1/0	3/1/0	5/0/1	58	
	PO	1/0/0	2/3/0	2/1/1	2/3/0	1/0/0	1/1/1	1/1/0	2/0/0	1/3/0	3/2/0	2/0/2	36	$\bar{x}$ = 42.5
		5/0/0 (2.9%)	16/20/12	3/3/3	17/12/2	6/1/2 (57.1%)	6/7/1	3/3/0	8/0/0	7/7/0	9/5/0	8/1/3 (40%)		170
Mid (n=7)	HQ	0/1/0	XX	1/1/1	7/2/0	0/0/0	0/1/0	0/0/1	1/1/0	1/0/1	0/0/0	2/1/0	22	
	LL	0/0/0	0/2/0	XX	0/0/1	0/0/0	1/0/0	1/0/0	1/3/0	2/1/0	0/0/0	1/2/1	16	
	NY	0/0/0	1/0/0	1/1/0	XX	0/0/0	0/1/1	0/0/0	1/1/0	0/0/0	0/0/0	0/0/1	8	
	PS	0/0/0	1/0/0	1/0/0	2/0/0	XX	0/0/0	0/0/0	2/0/0	3/1/1	0/0/0	0/0/0	11	
	SK	0/0/3	3/2/0	1/0/0	2/0/1	0/0/0	3/0/0	1/0/1	1/0/1	2/0/0	0/0/0	0/0/0	21	
	ST	1/0/0	4/1/1	3/2/0	7/4/0	0/0/0	11/1/0	0/0/0	4/0/0	3/5/0	3/2/0	13/2/0	67	
	WK	0/0/0	9/7/2	3/0/0	5/2/0	1/1/0	9/5/2	4/0/1	2/3/0	5/7/1	0/1/1	9/0/1	81	$\bar{x}$ = 32.3
		1/1/3 (2.2%)	18/12/3	10/4/1	23/8/2	1/1/0 (36.7%)	24/8/3	6/0/3	12/8/1	16/14/3	3/3/1	25/5/3 (61.1%)		226
Low (n=12)	AL	0/0/0	1/0/0	1/0/0	7/0/1	0/0/0	2/0/1	0/0/2	6/1/0	3/4/0	8/1/0	6/0/2	46	
	CO	0/0/0	6/0/0	0/0/0	3/1/2	0/2/0	XX	0/1/1	1/2/2	5/2/7	1/2/0	3/0/2	43	
	DD	0/0/0	3/0/0	0/0/0	2/0/1	0/0/0	1/1/0	2/0/0	1/1/0	1/1/0	1/0/0	0/0/1	16	
	LS	0/0/0	0/0/0	0/1/0	0/0/1	0/0/0	0/0/0	XX	0/1/0	0/0/0	0/0/0	0/0/0	3	
	LY	0/0/0	0/1/0	0/0/0	0/0/0	0/0/0	0/0/0	1/0/0	0/0/1	0/0/0	0/0/0	2/0/1	6	
	MH	0/0/0	0/2/2	0/0/2	1/0/1	2/1/0	2/0/0	3/3/3	0/4/3	XX	0/1/1	1/0/0	32	
	ML	0/0/0	0/0/1	0/1/0	0/1/0	0/0/0	0/0/0	0/2/0	XX	0/2/2	0/0/0	0/0/1	10	
	MM	0/0/0	0/0/0	0/0/1	0/0/1	1/0/0	0/0/0	0/0/0	3/0/1	0/0/0	XX	5/1/0	13	
	PA	0/0/0	4/3/2	1/0/0	3/2/0	1/0/0	1/0/0	0/0/0	1/0/3	6/1/1	1/0/0	2/0/1	33	
	PH	0/0/0	0/0/0	0/0/0	1/1/1	0/0/0	0/0/0	0/0/0	0/1/0	0/0/0	2/0/0	XX	6	
	PT	0/0/2	4/3/3	0/0/1	0/1/1	2/0/1	0/0/0	2/0/1	0/0/0	5/6/2	0/2/0	2/1/4	43	
	RS	1/0/0	0/1/0	6/0/0	1/1/1	0/0/0	2/0/0	2/0/0	2/0/0	5/1/0	2/1/0	4/1/0	31	$\bar{x}$ = 23.5
		1/0/2 (1.1%)	18/10/8	8/2/4	18/7/10	6/3/1 (33.7%)	8/1/1	10/6/7	14/10/10	25/17/12	15/7/1	25/3/12 (65.2%)		282
Infant totals		7/1/5	52/42/23	21/10/8	58/27/14	13/5/3	38/16/5	19/9/10	34/18/11	48/38/15	27/15/2	58/9/18	678 (375 approaches + 303 attempts/ successes)	
Rank totals		13		275 $\bar{x}$ = 68.75						390 $\bar{x}$ = 65			$\bar{x}$ = 29.5	

*Table I presents an approaches/attempted/successful infant handling episodes matrix. Females are alphabetical within their dominance categories. Infants are alphabetical within mothers' dominance hierarchy categories. Empty cells (represented by XX) indicate a mother–infant pair. Also shown in this table are totals for each female, totals for each infant, totals and means for the three females' dominance ranking categories, and totals and means for the three infants' mothers' dominance ranking categories.

TABLE II. Totals Used in 3×3 and 3×2 Contingency Tables for Permutation Tests

Data	All (A)			Approaches (B)			Attempted (C)[a]			Successful (D)[a]		
Mother's rank	H	M	L	H	M	L	H	M	L	H	M	L
Handler's rank												
High	5	97	68	5	42	41	0	**36**	**23**	0	**19**	**4**
	(2.9%)	(57.1%)	(40%)	(5.7%)	(47.7%)	(46.6%)	(0%)	**(64.93%)**	**(35.07%)**	(0%)	**(82.61%)**	**(17.39%)**
Mid	5	83	138	1	52	86	1	**25**	**38**	3	**6**	**14**
	(2.2%)	(36.7%)	(61.1%)	(0.7%)	(37.4%)	(61.88%)	(1.6%)	**(39.06%)**	**(59.34%)**	(13.04%)	**(26.09%)**	**(60.87%)**
Low	3	95	184	1	50	97	0	**22**	**44**	2	**23**	**43**
	(1.1%)	(33.7%)	(6.52%)	(0.68%)	(33.78%)	(65.54%)	(0%)	**(33.33%)**	**(66.67%)**	(2.94%)	**(33.82%)**	**(63.24%)**

[a] Bold numbers in columns C and D reflect a summary of the data used in the 3×2 permutation tests.

ture [Dow and de Waal, 1989; Knox & Sade, 1991]. Dagosto [1994, p. 192] used randomization tests in a study of lemur behavior, arguing that "[S]uch tests are becoming more popular in ecological and evolutionary studies, partly for the reason that it is often particularly difficult to justify the assumption of random sampling." Dagosto [1994] showed that permutation tests take into account the repeated measures or clustering effects we note above. Mundry [1999] also employed permutation tests for complicated (i.e., missing values), repeated measures quantitative data. Both Mundry [1999] and Dagosto [1994] include extended explanations of randomization/permutation tests and provide extensive references to the use of these methods. (We also refer the reader to Manly [1991] and Good [2000] for particularly effective general discussions of randomization/permutation tests.)

To understand the logic of the permutation test for our data set, we investigate the following formulation of the null hypothesis to our first research hypothesis.

> H_0. Handlers interacted with the infants as given in the data set. These interactions involved a variety of complex causes, but this complexity was independent of female rank. Ranks can be viewed as meaningless labels attached to handlers and mother–infant pairs.

The null hypothesis posits a random nature to ranks, which we employ in constructing, through a process of simulation, the sampling distribution of a test statistic.

Computing Permutation Distributions

We began by computing permutation distributions for the 3 × 3 tables formed from the "attempted" and "successful" data presented in the Table I frequency matrix and summarized in Table II, columns C and D. Although these are not the data upon which our final analyses are based (see discussion of 3 × 2 tables later in this section), the permutation process is easier to understand by starting with a 3 × 3 explanation. Thus, for the 3 × 3 tables, the randomization/permutation distribution was computed in the following manner.

1. We assign ranks at random to the mother–infant pairs (i.e., assigning randomly but maintaining the 1 High, 4 Mids, and 6 Lows distribution within the 11 pairs) as seen in Table I.
2. We assign ranks at random to the remaining non-mother females (i.e., assigning 3 Highs, 3 Mids, and 6 Lows randomly but maintaining the original distribution of 4 Highs, 7 Mids, and 12 Lows overall) as seen in Table I.
3. We thus have the original data table and distribution of ranks, except that the possessors of the ranks have changed.
4. We reform the 3 × 3 table.
5. We compute the test statistic.

By randomizing/permuting the original distribution of ranks to the mother–infant pairs and non-mother females, clusters of interactions remain intact. If ranks bear no relationship on the handling of infants by females, then a test statistic that measures strength of relationship in some way should not be unusually large for our data set with respect to all tables that could occur through permutations of this distribution of ranks. The permutation test measures the strength of relationship by computing the probability of a particular result (i.e., the distribution seen in the data) occurring by chance.

Consider the research hypothesis that handlers tend to handle infants of females ranked similar or lower than themselves. A natural test statistic that is large for tables corroborating the research hypothesis is a linear combination statistic we will denote by **W** that would look like this:

W (the sum of the entries of) =

$$\begin{bmatrix} a & d & g & & 1 & 1 & 1 \\ b & e & h & \times & -1 & 1 & 1 \\ c & f & i & & -1 & -1 & 1 \end{bmatrix} = a + d + g - b + e + h - c - f + i = \mathbf{W}$$

The **W** test statistic is monotonic with the research hypothesis. That is, it is larger for data sets strongly in the direction of the research hypothesis, and smaller for data sets that either support the null or differ from the null in directions counter to the research hypothesis. For example, in the two hypothetical 3 × 3 tables shown below, the first table is clearly more strongly supportive of the research hypothesis than is the second (**W** = 518 vs. **W** = 168).

Hypothetical Data Example

Handler		Mother							
	High	Mid	Low						
High	15	92	63		15	92	63		
Mid	5	83	138	=	–5	83	138	=	518
Low	0	75	207		–0	–75	207		
	0	67	103		0	67	103		
	5	83	138	=	–5	83	138	=	168
	100	150	32		–100	–150	32		

An advantage of randomization tests is that there is flexibility in the choice of test statistic. Many test statistics will maintain accuracy when the null is true, but certain test statistics will be more powerful toward the research (i.e., alternative) hypothesis. (See Efron and Tibshirani [1998] on this point.) In this case we have chosen **W** precisely because of its property of being monotonic with the research hypothesis. We are not making predictions about any particular cell in the table. For example, if the middle row of the first example read –5, 138, 83, the test statistic would still be 518 and the research hypothesis would be just as strongly supported. However, as we will demonstrate later, the very flexibility of this statistic does allow one to look at various options relatively easily.

Computing the Attempts and Successes Permutation Distributions

However, there was one further complication in our data that had to be addressed before the permutations could be computed. There was only one high-ranking infant during the data collection period. The presence of only one high-ranking infant meant very few opportunities for handlers to interact with a high-ranking infant. To address the potential bias introduced by this one infant, we removed him and his interactions from the data analyzed. Doing so left us with all of the handlers (23 ♀ in three ranking categories) and one less mother–infant pair (10 pairs in two ranking categories), and, thus, data that formed 3 × 2 tables. The permutation distributions were computed as described previously with the following changes:

1. …. (… maintaining the 4 Mids and 6 Lows distribution with the 10 pairs).
2. Same.
3. We thus have the original data less those interactions with the high-ranking infant.
4. … 3 × 2 table.
5. Same.

The permutation tests work by generating many random data sets through random assignment of ranks to handlers and mother–infant pairs. We would expect that our observed values of **W** would not look unusual among the values generated if our null hypotheses were true. Alternatively, if our observed values were in the right-hand tail of this simulated permutation distribution, we would have grounds for rejecting the nulls. Following Dagosto [1994], Mundry [1999], and others, 10,000 permutations were run for each of the tests described below. The level of significance for these tests was set at $P = 0.05$. P-values for permutation tests are very computer-intensive. The margins of errors for these P-values will vary but will be about 0.005 or less (95%) when the true P-value is 0.05. Calculations for all permutation tests used the PC Splus 2000® software package.

RESULTS

We recorded a total of 303 attempted/successful infant handling episodes during the period of November 1991 through September 1992. The complete data set, including all attempts/successes and approaches (which are not discussed), is presented in Table I.

As can be seen, there is considerable individual variation for both mother–infant pairs and females in the number of handling episodes received and committed, respectively. While some mother–infant pairs were very “popular,” others were much less so. Similarly, while some females were frequent handlers, others did so very infrequently. However, all of the focal females were handlers and all of the infants the recipients of attempted and/or successful handles.

These data are categorical and can be summarized for descriptive purposes using contingency tables. Table II shows totals (taken from Table I) used in 3 × 3 tables of mother ranks by handler ranks for the interactions. The column A data represent all interactions (approaches + attempted + successful). Columns B, C, and D present the data by the type of interaction. The bold numbers in columns C and D reflect a summary of the data used in the 3 × 2 permutation tests.

Effects of Rank

All 23 focal females attempted and/or successfully (attempted/successful) handled more than one unrelated infant. The number of infant *partners* per a particular female varied (range = 1–9, $\overline{x} = 5.6$ infant partners) with a total of 129 unique dyads (of a possible 242) represented. The number of infant *interactions* by a given focal female also varied greatly (range = 2–31, $\overline{x} = 13.2$). It is obvious that all females did not interact with the same infants and the composition of female–infant dyads was not random. Most females appeared to have one to three “favorite” infants that received most of their attempted/successful handles.

However, the apparent effects of dominance ranking category (both the female’s and the mother’s) on infants attempted/successful handles are modest, at best. The Table I frequency matrix reveals that 100% of the infant attempted/successful handles by high-ranking females are with infants of mid- or low-ranking mothers. This preference, however, is complicated by the factor, mentioned earlier, of only one high-ranking infant available with which they could have interacted. Similarly, while 95.4% of the infant attempted/successful handles by mid-ranking females are with the infants of mid- and low-ranking females, 90.9% of the infants are of mid- and low-ranking mothers. Finally, while 64.9% of the attempted/successful handles by low-ranking females are with infants of low-ranking mothers, again, 54.5% of the infants available are of low-ranking mothers. Thus, these data represent only modest differences from what one might expect given the distribution of infants. However, given that these differences are in the direction predicted by the research hypothesis, and given that one would expect females' ranks to play a role in these interactions, we deemed the data worthy of some further consideration via the permutation tests.

We therefore examined the attempts and successes as described in the previous section to determine if females are more likely to handle "same or lower" infants. We calculated **W** for each 3 × 2 table (see Table II, bold numbers in C and D), which showed that while there was a statistically significant effect of rank on attempted handles ($P = 0.0498$) there was not a significant effect with successful handles ($P = 0.5128$). However, if one refers back to the visual presentation (1's and –1's) of **W** in the previous section and looks at the arrangement of "–'s" in the last two columns, it becomes apparent that what **W** is actually testing is whether the one "–" cell is different from the other five cells. We therefore refined our statistic, as a form of post hoc analyses, to ask two more finite questions of the data: 1) whether females are more likely to handle "lower" (rather than "same or lower") ranked infants, and 2) whether females are more likely to handle "immediately lower" ranked infants.

The statistical answers to both of these questions were "no" (attempts—lower: $P = 0.264$, immediately lower: $P = 0.1314$; successes—lower: $P = 0.2608$, immediately lower: $P = 0.416$). While the first round of permutations showed a barely significant effect of dominance rank on attempts, further refinement of the analyses showed that this effect was probably due to what we were actually asking **W** to test rather than a true effect. Thus, it appears that Mchelelo females are not more likely to attempt or successfully handle infants ranked "same or lower," "lower," or "immediately lower" than themselves. The lack of significance within the successful handles is not particularly surprising given that the ratio of *attempted* to *successful* handles of 1.9:1, i.e., there are almost twice as many attempts as there are successful handles. Further subdivision of the successful handles data also failed to show significant effects (i.e., ≤ 1 mo, $P = 0.1291$; >1 m, $P = 0.6932$). (See Table III for a summary of the permutation test results outlined above.)

Thus, the Mchelelo females are also not particularly successful at handling even the very youngest infants of similar/lower-ranked females, i.e., rank offers no significant privileges with this infant age category. This finding, as well, is not particularly surprising given an attempted to successful ratio of 3.3:1 during the infant's first month. Newborn infants are obviously very attractive to most or all of the female handlers, as is evidenced by over one third (34%) of all the recorded attempts and successful handles occurring during the infant's first month. However, mothers are quite skillful in preventing successful handles of their infants during this period and handler's rank does not offer significant privileges with regard to the likelihood of being successful, i.e., of 104 observed attempted/successful handling episodes that occurred during the infants' first month, only 24 (23.1%) were successful. Mothers were able to prevent other females from successfully handling their infants almost 80% of the time—and they were doing so despite the fact that these attempts were often from higher ranking females.

TABLE III. Summary of *P*-Values From Permutation Tests

Question	Data set	*P*-value for **W**
Same or lower	Attempts	0.0498
	Successes	0.5128
	$i \leq 1$ month of age	0.1292
	$i > 1$ month of age	0.6932
Lower	Attempts	0.264
	Successes	0.2608
Immediately lower	Attempts	0.1314
	Successes	0.416

DISCUSSION

Infant handling is a heterogeneous phenomenon at both the intraspecies and interspecies levels [Maestripieri, 1994; Mitani & Watts, 1997; Paul, 1999]. While most primate females are attracted to young infants, the degree to which females act on this attraction, and the degree to which mothers tolerate other females interacting with their infants varies greatly [Hrdy, 1999]. Numerous social and ecological factors, such as kinship, group size, and predation risk, may influence how a mother reacts to infant-handling overtures. Here, we have focused on one such factor—dominance rank—and its correlation with those infants with which the adult females interact, and the success of those interactions in a yellow baboon population.

Given the current state of knowledge of yellow baboon females' social relationships [Altmann, 1980; Hausfater et al., 1982; Wasser, 1983] and our knowledge of this particular population [Bentley-Condit & Smith, 1997, 1999], we hypothesized that the dominance ranks of the handler female and the infant's mother would significantly influence infant-handling interactions. Specifically, given the linear and transitive female dominance hierarchy in this population, we predicted that females would tend to handle the infants of females similarly or lower ranked them themselves.

However, in applying the permutation test analyses, the expected outcomes were not realized. While we did find a barely significant effect of rank on attempts for "same or lower," this effect disappeared under the conditions of "lower" and "immediately lower." As well, there were no discernable rank-related differences in successfully handling infants. In fact, on average, low-ranked handlers experienced just as many successes as did high-ranked handlers (LO $\bar{x} = 5.67$ vs. HI $\bar{x} = 5.75$).

This lack of benefit of rank in this situation further elucidates—or perhaps complicates—the ongoing discussions of dominance ranks and their meanings and relevance. Bernstein [1981] was one of the first to draw to our attention that rank is a relationship, not an absolute. As such, dominance is a negotiated reality that is to some degree renegotiated in different situations. That dominance rank means nothing in this population's infant-handling interactions demonstrates that the priority of access model [Seyfarth, 1977] does not necessarily apply to all "resources." Despite the desirability of a young infant and despite the limited nature of this resource, higher-ranked females are not more successful. In this respect, our findings are similar to those of Manson [1999] with white-faced capuchins. There are thus some contested situations in which rank does not prevail. One might also interpret these data as showing that when potential costs are very high, i.e., the safety of one's infant is at stake, females in this population are willing to risk the displeasure of a higher-ranked female. However, unfortunately, our data set is too small to allow us to adequately examine either the functions or motivations behind these interactions (see Maestripieri [1994] for a discussion of function hypotheses).

While the preceding paragraphs help to illuminate the lack of importance of dominance rank's effects on handling within this population, many questions still remain. First, we are left to wonder what does determine with which infants an adult female baboon will interact. A quick glance at Table I supports our interpretation that females had their "favorite" infant interaction partners. If rank is not the determining factor for interaction partner, then there must be some other explanation(s). Yet to be explored with these data are the effects of other aspects of a female's social relationships and network (e.g., the impact of being a preferred proximity partner or a preferred grooming partner on a female's abilities to attempt to or successfully handle an infant).

We can state that while the infant-handling interactions were obviously distressful to both infant and mother, none were ever abusive in nature. Thus, the Mchelelo females' handling interactions appear to be somewhat "kindler and gentler" than those reported for other populations/species [Hrdy, 1976; Wasser & Barash, 1981]. The affiliative nature of these interactions also indicates that this population does not fit with Maestripieri's [1994] assertions that species with within-group contests for food, despotic female dominance relationships, and low tolerance of infant handling should have a high proportion of abusive vs. affiliative infant-handling interactions. As well, there were no real differences in frequency between parous and nulliparous handlers for either attempts or successes (parous: attempts $n = 137$, $\bar{x} = 8.56$, successes $n = 76$, $\bar{x} = 4.75$; nulliparous: attempts $n = 52$, $\bar{x} = 7.43$, successes $n = 38$, $\bar{x} = 5.43$). These qualitative data reflect upon possible functions of infant handling (i.e., intentional harm, learning to mother), another issue in need of further investigation.

Finally, we see our utilization of permutation distributions to test our findings to be just as important as our actual findings regarding infant handling. The permutation tests allow the researcher to test for significance where tests such as chi-square are not appropriate, as the permutations make few assumptions and can handle complicated data sets. They provide flexibility in examining specific research hypotheses, and are run relatively easily with statistical software such as PC Splus 2000®. Given the complicated nature of most observational data, and the power of most desk and laptop computers, we foresee permutation tests rising in importance within the field of primatology and offering primatologists a new and more powerful data analysis tool.

ACKNOWLEDGMENTS

A preliminary report of these data was presented at the 1996 IPS/ASP conference in Madison, Wisconsin. We thank the Office of the President of Kenya for permission to conduct this research (#OP 13/001/20C 240/13) and the National Museums of Kenya and the Institute of Primate Research for technical support and assistance. Thanks also to K. Wilson, J. Larson, F. Muli, H. Jillo, and I. Jilloh for assistance in the field and with data collection. We also thank the *American Journal of Primatology* editor and anonymous *AJP* reviewers for their helpful and insightful comments. This project was supported by grants from the L.S.B. Leakey Foundation (V.B.-C.), the Mellon Foundation (V.B.-C.), Sigma Xi (V.B.-C.), the NSF (BNS-8921106) (E.O.S.), Emory University Research Committee (E.O.S.), and NIH (RR-00165) from the National Center for Research Resources to the Yerkes Regional Primate Research Center.

REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Altmann J. 1980. Baboon mothers and infants. Cambridge, MA: Harvard University Press. 242 p.

Altmann J, Hausfater G, Altmann S. 1988. Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 403–418.

Barton R. 1993. Sociospatial mechanisms of feeding competition in female olive baboons, *Papio anubis*. Anim Behav 46:791–802.

Bentley-Condit VK, Smith EO. 1997. Female reproductive parameters of Tana River yellow baboons. Int J Primatol 18:581–596.

Bentley-Condit VK, Smith EO. 1999. Female dominance and female social relationships in yellow baboons (*Papio hamadryas cynocephalus*). Am J Primatol 47:321–334.

Bernstein I. 1981. Dominance: the baby and the bathwater. Behav Brain Sci 4:419–457.

Bramblett C. 1981. Dominance tabulation: giving form to concepts. Behav Brain Sci 4:435.

Bullerman R. 1950. Note on kidnapping by bonnet monkey. J Mammal 31:93–94.

Collins D, Busse C, Goodall J. 1984. Infanticide in two populations of savanna baboons. In: Hausfater G, Hrdy SB, editors. Infanticide: comparative and evolutionary perspectives. New York: Aldine de Gruyter. p 193–215.

Condit VK, Smith EO. 1994. Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. Am J Primatol 33:57–64.

Dagosto M. 1994. Testing positional behavior of Malagasy lemurs: a randomization approach. Am J Phys Anthropol 94:189–202.

Dow M, de Waal F. 1989. Assignment methods for the analysis of network subgroup interactions. Soc Networks 11:237–255.

Efron B, Tibshirani R. 1998. An introduction to the bootstrap. Boca Raton: Chapman & Hall/CRC. 436 p.

Good P. 2000. Permutation tests: a practical guide to resampling methods for testing hypotheses. 2nd ed. New York: Springer. 270 p.

Hamilton W. 1964. The genetical evolution of social behaviour. II. J Theor Biol 7:17–52.

Hausfater G, Altmann J, Altmann S. 1982. Long-term consistency of dominance rank among female baboons. Science 217:752–755.

Hiraiwa M. 1981. Maternal and alloparental care in a troop of free-ranging Japanese monkeys. Primates 22:309–329.

Hrdy SB. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: Rosenblatt J, Hinde R, Shaw E, Beer C, editors. Advances in the study of behavior. Vol VI. New York: Academic Press. p 101–158.

Hrdy SB. 1978. Allomaternal care and abuse of infants among Hanuman langurs. In: Chivers D, Herbert J, editors. Recent advances in primatology. Vol I. Behaviour. London: Academic Press. p 169–172.

Hrdy SB. 1999. Mother nature: maternal instincts and how they shape the human species. New York: Ballantine Books. 723 p.

Hunt S, Gamache K, Lockard J. 1978. Babysitting behavior by age/sex classification in squirrel monkeys (*Saimiri sciureus*). Primates 19:179–186.

Knox K, Sade D. 1991. Social behavior of the Emperor tamarin in captivity: components of agonistic display and agonistic network. Int J Primatol 12:439–480.

Lancaster J. 1971. Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). Folia Primatol 15:161–182.

Maestripieri D. 1994. Social structure, infant handling, and mothering styles in group-living Old World monkeys. Int J Primatol 15:531–553.

Manly B. 1991. Randomization and Monte Carlo methods in biology. London: Chapman and Hall. 281 p.

Manson J. 1999. Infant handling in wild *Cebus capucinus*: testing bonds between females? Anim Behav 57:911–921.

Mitani J, Watts D. 1997. The evolution of non-maternal caretaking among anthropoid primates: do helpers help? Behav Ecol Sociobiol 40:213–220.

Mohnot S. 1980. Intergroup infant kidnapping in Hanuman langurs. Folia Primatol 34:259–277.

Moore T, Bentley-Condit VK. 2001. Using permutation tests to study infant handling by female baboons. STATS 31:7–14.

Mundry R. 1999. Testing related samples with missing values: a permutation approach. Anim Behav 58:1143–1153.

Nakagawa N. 1995. A case of infant kidnapping and allomothering by members of a neighbouring group in patas monkeys. Folia Primatol 64:62–68.

Nicolson NA. 1982. Weaning and the development of independence in olive baboons [dissertation]. Cambridge, MA: Harvard University. 163 p. Available from: University Microfilms, Ann Arbor, MI.

Paul A. 1999. The socioecology of infant handling in primates: is the current model convincing? Primates 40:33–46.

Rowell T, Hinde R, Spencer-Booth Y. 1964. "Aunt"–infant interaction in captive rhesus monkeys. Anim Behav 12:219–226.

Seyfarth R. 1977. A model of social grooming among adult female monkeys. J Theor Biol 65:671–698.

Small M. 1990. Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. Anim Behav 39:297–306.

Smuts BB. 1985. Sex and friendship in baboons. New York: Aldine de Gruyter. 303 p.

Strum SC. 1987. Almost human: a journey into the world of baboons. New York: Random House. 294 p.

Wasser S, Barash D. 1981. The selfish "allomother": a comment on Scollay and DeBold (1980). Ethol Sociobiol 2:91–93.

Wasser S. 1983. Reproductive competition and cooperation among female yellow baboons. In: Wasser S, editor. Social behavior of female vertebrates. San Diego: Academic Press. p 349–390.