

Kin Recognition by Paternal Half-Siblings in Captive *Papio cynocephalus*

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Our objective in this study was to evaluate whether a group of paternally related, subadult baboons (*Papio cynocephalus*) would preferentially interact with kin or nonkin when they had been raised apart from kin other than their mothers. Subjects and their mothers were removed from the breeding group and placed in alternate housing within 24 h after birth to ensure that the subjects would not have a social history with either their sire or their half-siblings. At 90 days of age, the 23 subjects were separated from their mothers and assigned to a peer–peer social group. Behavioral performance was measured using focal animal sampling techniques and 12 molecular behavioral criteria. Analyses of the data indicate that in dyadic interactions kin did not interact more frequently than nonkin in performance of affiliative, sociosexual, and agonistic behaviors. The hypothesis that baboons recognize kin in the absence of maternal associations was not supported by the data; moreover, we suggest that social learning and social history are the most likely mechanisms for kin recognition. *Am. J. Primatol.* 43:147–157, 1997. © 1997 Wiley-Liss, Inc.

Key words: kin selection; kin recognition; recognition mechanisms; *Papio*

INTRODUCTION

The theory of kin selection [Hamilton, 1964] predicts that individuals who behave in ways that increase the reproductive success of kin may increase the frequency of their own genes in succeeding generations, thereby raising their inclusive fitness. Individuals are more likely to help each other when the ratio of the recipient's benefits to the donor's costs is greater than the reciprocal of the degree of relatedness. Therefore, the ability to recognize and behave preferentially toward kin, particularly close kin, would be adaptive for the individual and its kin. Differential treatment of kin and nonkin is assumed to be evidence of kin recognition.

Kin recognition produced by familiarity because of prior association and/or spatial location has been cited as the most feasible mechanism for recognition of maternally related individuals (hereafter referred to as maternal kin recogni-

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tion) in nonhuman primates [Bernstein, 1991; Gouzoules, 1984; Walters, 1987]. Since this is not the case for paternally related individuals, more direct or innate mechanisms may be a likely possibility for paternal kin recognition. The ability to distinguish between individuals in this circumstance probably results from being able to detect a sufficient number of distinct cues found in individuals. If these cues are genetic, then relatedness can be detected [Grafen, 1990].

Previous kin recognition studies of paternally related nonhuman primates are few. However, the majority of primate groups contain several females who typically have single births and relatively long interbirth intervals (i.e., ≥ 1 year) and whose offspring are fathered by either one or only a few males. Because infants born in the same year might be half-siblings through the father, and therefore form a paternal sibship, more opportunities could result for sibling altruism through the paternal rather than the maternal line [Altmann, 1979].

A well-known example of primate kin recognition involves paternal half-sibling, infant pigtailed macaques (*Macaca nemestrina*) [Wu et al., 1980]. In this study, subjects were simultaneously exposed to two peers unknown to them, one an unrelated individual and the other a half-sibling. Results indicate that 13 of the 16 study subjects oriented toward and approached their paternally related but unfamiliar half-siblings significantly more often than unfamiliar nonrelatives. Originally this was thought to be evidence of phenotypic matching. The test situation, however, was not a natural one in that infants in the wild do not have to distinguish among strangers but among familiar group members [Walters, 1987]. In addition, prior to testing the study subjects were allowed to interact with nonrelatives, suggesting that the later preference for relatives, seen particularly in the older subjects, may be a result of mate choice in which animals chose mates slightly different from individuals with whom they are familiar with under natural conditions [Bateson, 1978, 1982, 1983]. Attempts to replicate the positive finding of the experiment by Wu et al. [1980] have failed [Frederickson & Sackett, 1984; Sackett & Frederickson, 1987]. These workers concluded that for juvenile macaques phenotypic matching did not influence the choice of a partner for spatial association and that the positive finding of Wu et al. [1980] was due to type I statistical error [Frederickson and Sackett, 1984; Sackett and Frederickson, 1987].

In a study comparing interactions between rhesus macaque (*Macaca mulatta*) infants and their full siblings, paternal half-siblings, and unrelated immatures, Small and Smith [1981] found that mothers resisted approaches by nonrelatives more than approaches by paternal half-siblings. However, the frequency of maternal resistance to the approaches of nonrelatives (34/92, or 37%) and half-siblings (16/49, or 33%) was virtually identical. The influence of confounding factors, such as dominance relations, was not considered in the study despite the importance of dominance rank in structuring the relationships of mothers and infants with other group members [Gouzoules, 1984]. Further, paternal half-siblings are not related to the mother; thus, it is not logical that a female would permit individuals unrelated to herself to approach and possibly harm her infant [Bernstein, 1991].

In order to provide additional information on the nature of kin selection and kin recognition behavior, we designed an experiment to evaluate whether paternally related, subadult baboons (*Papio cynocephalus*; thirteen males and ten females) would preferentially interact with either kin or nonkin in a situation where they were unfamiliar with the identity of their relatives other than their mothers. We tested the hypothesis that relatedness (kin or nonkin) and gender would affect the rate of dyadic interactions.

In this study, *kin recognition* is defined as the ability to identify or categorize

conspecific individuals as either kin or nonkin. This contrasts with *kin discrimination*, which refers to the ability to recognize various categories of relatives (e.g., full sibling vs. half-sibling or aunt vs. grandmother). Although in studies of kin recognition the terms *recognition* and *discrimination* are often used interchangeably [Gouzoules, 1984; Lacy & Sherman, 1983; Wilson, 1987], the distinction between these two terms has important behavioral and evolutionary consequences.

MATERIALS AND METHODS

Subjects

The 23 subjects (thirteen males, ten females) used in this study were born into the primate colony at the Southwest Foundation for Biomedical Research (SFBR). These baboons (*Papio cynocephalus*) are members of a single species represented by five polytypic and interbreeding subspecies [Buettner-Janusch, 1966; Nagel, 1974; Terry, 1977] and are also referred to as savanna baboons. The six sires and twenty-three dams of the study subjects were obtained from several East African trapping sites.

Experimental Design

To ensure that the subjects would not have a social history with either their sires or half-siblings, we removed subjects and their mothers from the breeding group and placed them in alternate housing within 24 h after birth. At 90 days of age, the infants were assigned to a peer-peer social group consisting only of the 23 subjects in an indoor nursery. Each individual was housed with approximately four kin (half-siblings) and approximately eighteen nonkin. At 6 months of age, the study group was moved to an outdoor cage measuring 15 × 7 × 8 m. Additional details of the early housing protocols are described by Young and Bramblett [1977] and Coelho and Bramblett [1981, 1990].

Data presented in this paper were collected when the subjects were between 43 and 83 months of age. Males at this age are probably able to produce viable sperm, but full skeletal and muscular growth, development of the shoulder mantle, complete eruption of the canine teeth, and behavioral development have not been completed [Altmann et al., 1981; Coelho, 1985; Strum, 1991; Watts, 1990]. In their natural habitats, this is the time that males begin to emigrate from their natal troops [Hall & DeVore, 1965]. At the same age, females have attained menarche [Altmann et al., 1981; Coelho, 1985; Strum, 1991; Watts, 1990] and behave as an adult [Hall & DeVore, 1965]. Female baboons stay in their natal troops and develop dominance relations along the lines of familial memberships [Hall & DeVore, 1965].

Behavioral Methods and Measures

The methods and measurement techniques used in this study are documented in a number of publications from the Behavioral Medicine Laboratory at SFBR [for a review see Coelho & Bramblett, 1990]. As criteria for measuring possible differences in dyadic performance between kin and nonkin, 12 of the most frequently observed behaviors were chosen from an ethogram developed by Coelho and Bramblett [1990]. The 12 criteria are contact, groom, proximity, follow, lipsmack, social approach, charge, displace, hip touch, present, aid/assist, and enlist (see Table I). These behaviors are molecular components of affiliative, approach, attack, threat, and sexual behavior categories [Coelho & Bramblett, 1990].

TABLE I. Behavioral Measures [Coelho & Bramblett, 1990]

Affinitive behaviors	
Contact:	Passive touching of an animal; nonextensive bodily contact
Groom:	Cleaning or manipulation of the hair or skin of an animal
Proximity:	An actor occupies a stationary position within 1 m of one or more stationary animals
Approach behaviors	
Follow:	Any locomotor action which permits an actor to shadow a recipient at a slow to moderate walking pace
Lipsmack:	Rapid, repetitive opening and closing of lips; may also include opening and closing of lips on a flattened and projecting tongue
Social approach:	An actor unhurriedly advances toward a recipient seemingly with the goal of social interaction, which may or may not be realized
Attack behaviors	
Charge:	Rapid forward movement towards a recipient who is stationary
Displace:	An actor supplants a recipient and occupies the space vacated by the recipient
Sexual behaviors	
Hip touch:	The placing of one hand on the hip of a recipient
Present:	A quadrupedal stand, positioning of the anogenital region within the tactile range of another animal that is in proximity
Threat behaviors	
Aid/assist:	An actor lends support to a recipient in attacking or threatening a third animal
Enlist:	An actor seeks aid from a second animal in threatening or attacking a third animal by glancing from the second animal and looking towards the third animal

Behavioral sampling was carried out over a 12 month period by a pair of full-time observers using focal animal sampling [Altmann, 1974]. Data acquisition sessions were designed to obtain an equal sample of behaviors between 0800 and 1700 h and over every month for each subject throughout the study period [Coelho & Bramblett, 1981, 1990]. Observers were blind with respect to the relatedness of the study subjects and always maintained at least a 90% level of interobserver agreement. Data were derived from approximately 820 focal animal sampling sessions (each 10 min in duration), and each subject was observed approximately 36 times (range = 27–49 focal sessions). Behavioral measures consisted of frequency of behaviors observed and were expressed as rates per hour of sampling by kin and nonkin.

Data Analyses and Statistical Treatment

We performed two-factor ANOVA to evaluate the effects of relatedness and gender. We tested the hypothesis that relatedness (kin or nonkin) and gender would affect the rate of dyadic interactions. Specific null hypotheses tested for each of the behavioral measures were 1) H_0 , no differences in dyadic interaction between kin and nonkin, and 2) H_0 , no differences in dyadic interaction between males and females.

The housing protocol used for this study necessitated investigating cohort effect. Cohort is the combined effects of age, body size, and temporal peer grouping. In other words, cohort indicates the point in time when the subject was born during the course of the experiment and reflects the individual's relative body size and maturation in comparison to other subjects in the same social group. Stepwise multiple regression was used to compute the relative contribution of cohort to variance in rates of behavioral performance for each molecular behavior. All cohort results were nonsignificant.

RESULTS

The hypothesis that baboons recognize kin in the absence of maternal association was not supported by our data. The study subjects did not demonstrate statistically significant preference for dyadic frequency of interacting with kin or nonkin for any of the twelve behaviors in this sample (see Tables II–VI). Females did not exhibit preference for interaction with their female kin or their male kin, and males did not exhibit preference for interaction with their male or female kin.

We found consistent performance differences for gender-specific affiliative, sociosexual, and agonistic behaviors (see Tables II–VI). Specifically, females had higher performance rates for groom and present, while males had higher rates for follow, chase, displace, and hip touch. These results are in agreement with previous studies of savanna baboons which report early development of gender differences for these behaviors [Coelho & Bramblett, 1981; Ransom & Rowell, 1972; Young et al., 1982]. Thus, experience with adult males and females was not necessary for species-typical gender differences to develop in the study subjects.

DISCUSSION

Numerous authors have argued that the ability to recognize kin from nonkin must have mechanisms that permit its evolution [for a review see Blaustein & Porter, 1990; Fletcher & Michener, 1987; Wilson, 1987]. Some mechanisms are thought to have a genetic basis (e.g., recognition alleles), while others such as phenotypic matching may result when an individual learns and recalls the phenotypes of kin or of itself and then assesses similarities and differences between itself and an unfamiliar conspecific and the degree of relatedness [Blaustein, 1983; Hamilton, 1964; Holmes & Sherman, 1982]. This model is based on the

TABLE II. Dyadic Performance and Mean Rate Per Hour of Affinitive Behaviors*

Behavior	Gender	Kinship	Interaction
Contact			
F-test	.756	2.10	.645
P	.385	.148	.422
Groom			
F-test	7.59	.731	1.31
P	.006	.393	.253
Proximity			
F-test	1.09	3.46	.836
P	.298	.064	.361
Behavior	Kin	Nonkin	Total
Contact			
Females	.032 (.086)	.043 (.145)	.041
Males	.034 (.079)	.071 (.163)	.064
Groom			
Females	.262 (.568)	.180 (.412)	.195
Males	.101 (.314)	.113 (.263)	.111
Proximity			
Females	.300 (.342)	.347 (.412)	.337
Males	.306 (.404)	.445 (.494)	.421

*Standard deviations are included in parentheses.

TABLE III. Dyadic Performance and Mean Rate Per Hour of Approach Behaviors*

Behavior	Gender	Kinship	Interaction
Follow			
F-test	7.16	.618	1.62
<i>P</i>	.007	.432	.204
Lipsmack			
F-test	2.19	.079	.695
<i>P</i>	.140	.779	.405
Social approach			
F-test	.850	1.33	.955
<i>P</i>	.057	.249	.329
Behavior	Kin	Nonkin	Total
Follow			
Females	.075 (.151)	.047 (.143)	.052
Males	.155 (.362)	.271 (.688)	.251
Lipsmack			
Females	.057 (.117)	.045 (.090)	.047
Males	.070 (.162)	.094 (.240)	.090
Social approach			
Females	.446 (.587)	.458 (.580)	.456
Males	.317 (.495)	.462 (.619)	.437

*Standard deviations are included in parentheses.

presumption that phenotypic and genotypic similarity are correlated and that the phenotypic marker (e.g., a particular odor or vocalization) may have genetic and/or environmental components. Recognition alleles are hypothesized to encode a phenotypic marker and the knowledge or ability to recognize the cue in others independent of learning, leading to the differentiation of kin from nonkin [Blaustein, 1983]. Recognition alleles have been metaphorically referred to as the “green beard effect” which essentially says, “I have a green beard, and I will behave preferentially or altruistically to others who have green beards” [Dawkins, 1982].

TABLE IV. Dyadic Performance and Mean Rate Per Hour of Attack Behaviors*

Behavior	Gender	Kinship	Interaction
Charge			
F-test	5.75	1.22	.003
<i>P</i>	.017	.270	.953
Displace			
F-test	11.9	.334	.755
<i>P</i>	.001	.068	.385
Behavior	Kin	Nonkin	Total
Charge			
Females	.002 (.011)	.015 (.071)	.013
Males	.030 (.074)	.042 (.127)	.042
Displace			
Females	.011 (.035)	.024 (.074)	.022
Males	.047 (.131)	.085 (.148)	.078

*Standard deviations are included in parentheses.

TABLE V. Dyadic Performance and Mean Rate Per Hour of Sexual Behaviors*

Behavior	Gender	Kinship	Interaction
Hip touch			
F-test	6.85	.037	.609
<i>P</i>	.009	.847	.435
Present			
F-test	4.58	.736	.753
<i>P</i>	.033	.391	.386
Behavior	Kin	Nonkin	Total
Hip touch			
Females	.020 (.071)	.012 (.048)	.014
Males	.046 (.096)	.059 (.160)	.057
Present			
Females	.169 (.338)	.369 (1.67)	.333
Males	.021 (.105)	.020 (.084)	.020

*Standard deviations are included in parentheses.

An alternative strategy for kin recognition would be to assume that close associates are kin and behave as if they were. This strategy would be based on patterns of familiarity resulting from prior association and spatial location and may not include a genetic component [for a review see Blaustein & Porter, 1990; Holmes & Sherman, 1982; Fletcher & Michener, 1987; Wilson, 1987]. Recognition by these mechanisms is indirect since kin may not be actually recognized per se, but those who are most likely to be kin are those who are most likely to be groomed, defended, or aided in some way [Blaustein, 1983]. However, it would be reasonable to assume that recognition errors may occur with these mechanisms [Bernstein, 1991; Walters, 1987]. In spatial location, the individual recognizes kin on the basis of cues in the environment (e.g., nest site or home territory), not on cues presented by its conspecifics. Individuals encountered in or within a certain distance of the particular environmental cue are responded to as kin, while those encountered outside are treated as nonkin. The most widespread and important mechanism for kin recognition in mammals appears to be famil-

TABLE VI. Dyadic Performance and Mean Rate Per Hour of Threat Behaviors*

Behavior	Gender	Kinship	Interaction
Aid/assist			
F-test	.162	1.17	.117
<i>P</i>	.688	.280	.733
Enlist			
F-test	1.03	1.38	.153
<i>P</i>	.311	.242	.696
Behavior	Kin	Nonkin	Total
Aid/assist			
Females	.000 (.000)	.022 (.140)	.017
Males	.012 (.044)	.023 (.070)	.021
Enlist			
Females	.000 (.000)	.021 (.000)	.016
Males	.018 (.018)	.029 (.067)	.026

*Standard deviations are included in parentheses.

ilarity through prior association [Bekoff, 1981; Sherman, 1980]. During development, individuals learn and respond to cues from the most familiar or most commonly encountered conspecifics in their environment. Individuals respond to familiar individuals as kin and unfamiliar individuals as nonkin.

Maternal kin social interaction has been proposed as the most feasible mechanism for kin recognition for nonhuman primates [Bernstein, 1991; Gouzoules, 1984; Walters, 1987], because it is thought that individuals who have rarely coexisted historically should not distinguish each other from unrelated individuals [Sherman, 1980, 1981]. In the majority of nonhuman primate species, the infant is continually associated with its mother for the first part of its life [Walters, 1987]. This bond persists after the birth of the mother's next infant and often endures for many years (especially with female offspring). As a consequence, infants will be in proximity to older siblings and possibly other maternal relatives as well. Mutualism and reciprocal altruism may develop among these individuals, and their relationships will be selected for as predicted by the inclusive fitness theory [Bernstein, 1991].

In a variety of primate taxa, mother-offspring and sibling relations can be distinguished from those of other group members for a variety of social behaviors. For example, individuals engaged in physical contact, grooming, spatial proximity, or agonistic aiding have been reported to more likely to be maternal kin than would be expected by chance [Baker & Estep, 1985; Berman, 1982; Colvin, 1983; Colvin & Tissier, 1985; Ehardt & Bernstein, 1986; Ehardt & Bramblett, 1980; Fairbanks & McGuire, 1985; Glick et al., 1986a,b; Koyama, 1985; Loy & Loy, 1974; Nash, 1978; Quiatt, 1986; Rosenblum, 1971; Sade, 1965; Silk, 1982, 1984; Silk et al., 1981; Taylor & Sussman, 1985; Walters, 1981]. However, the proximal mechanism for recognition in these cases is based on early patterns of familiarity rather than other more direct recognition mechanisms such as phenotypic matching or recognition alleles.

While there has been no clear evidence of paternal kinship correlating with behavior in nonhuman primates [Bernstein, 1991; Gouzoules, 1984; Walters, 1987], few studies addressing paternal kin recognition have been attempted [Bernstein et al., 1981; Frederickson & Sackett, 1984; Small & Smith, 1981; Wu et al., 1980]. Unlike the situation with maternal kin, nonhuman primates may not be able to recognize paternal kin from social interactions; therefore, genetically based recognition mechanisms may be feasible. It is important to note that although maternal kin recognition (kin-associated behavior between mother, offspring, and siblings) has been well documented for nonhuman primates, reports of matrilineal kin recognition (kin-associated behavior that discriminates between more distant categories of relatives, e.g., cousins, great-aunts, great-grand-offspring from nonrelatives) are few [Gouzoules, 1984].

In this study we wanted to determine whether subadult savanna baboons (*Papio cynocephalus*) would preferentially interact with kin or nonkin in a condition where they did not have the opportunity to learn the identity of their kin through maternal associations. The elimination of these types of learning opportunities resulted in an ideal situation for testing whether a recognition mechanism other than prior association and/or spatial location could mediate recognition of paternal half-siblings. Unlike previous studies of paternal kin recognition, the current study used behaviors that would normally be directed preferentially toward kin, such as contact, grooming, aid/assist, and enlist, and other behaviors which would presumably be directed toward nonkin, such as hip touch and present. Nevertheless, we found that the study subjects did not demonstrate statistically significant preference for interacting with kin or nonkin for any of the

behaviors in this sample. The results of this study, therefore, do not point to genetically based cues [Blaustein, 1983; Hamilton, 1964; Holmes & Sherman, 1982] as mechanisms of kin recognition for these paternally related subjects.

However, it is unclear whether the ability to categorize individuals as kin or nonkin is necessary for kin selection to work. In most nonhuman primate species, an infant is continually associated with its mother for the first part of its life and as a consequence has prolonged exposure to other maternal kin, including older and younger siblings and possibly aunts and the mother's mother. An infant's early social relationships, then, are almost all with maternal kin. Thus, selection for these maternal relationships may be the most parsimonious mechanism for explaining kin selection for savanna baboons and other nonhuman primates which share the same social organization [Bernstein, 1991; Fedigan, 1982; Walters, 1987]. This conclusion is supported by errors in kin recognition of unrelated adopted infants and close associates of the mother who receive the same preferential treatment as maternal relatives. We propose that, if and when nonhuman primates behave differentially with members of their social group, the basis of the observed recognition may be the result of social learning and social history.

CONCLUSIONS

1. In a condition in which kin is unknown by means of a learned social history, baboons did not demonstrate statistically significant preference for dyadic frequency of interacting with kin or nonkin for any of the 12 behaviors in this sample.
2. The hypothesis that baboons innately recognize kin was not supported by the data.
3. We suggest that social learning and social history are the most likely mechanisms for kin recognition in savanna baboons and other primates that share the same social organization.

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