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Behavior predicts genetic structure in a wild primate group

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ABSTRACT **The predictability of genetic structure from social structure and differential mating success was tested in wild baboons. Baboon populations are subdivided into cohesive social groups that include multiple adults of both sexes. As in many mammals, males are the dispersing sex. Social structure and behavior successfully predicted molecular genetic measures of relatedness and variance in reproductive success. In the first quantitative test of the priority-of-access model among wild primates, the reproductive priority of dominant males was confirmed by molecular genetic analysis. However, the resultant high short-term variance in reproductive success did not translate into equally high long-term variance because male dominance status was unstable. An important consequence of high but unstable short-term variance is that age cohorts will tend to be paternal sibships and social groups will be genetically substructured by age.**

In this study, we combined molecular genetic data with long-term behavioral and demographic data to examine several aspects of behavior-genetic relationships that are central to the evolution of primate social systems. The first of these is the priority-of-access model, which predicts that dominance status among adult males determines access to estrous females (1) and that variability in the number of offspring fathered by males will, therefore, directly reflect both the males' dominance status and the number of simultaneously estrus females (2). Second, we investigated the widespread assumption that short-term differences in mating success or paternity success are stable and, therefore, predictive of lifetime differences in reproductive success (for review, see refs. 3 and 4). Third, we examined the hypothesis that a species' dispersal system and social structure produce predictable population substructure within groups (5, 6). For example, adult males within groups of baboons and many other cercopithecine primates are predicted to be less closely related than are adult females, and relatedness should be greater within than between matrilines.

The study was conducted on a group of individually known wild savannah baboons, *Papio cynocephalus,* in Amboseli, Kenya (7). Like most cercopithecine primates and many other mammals (5, 8–11), these baboons live in polygamous multimale, multifemale social groups in which females are matrilocal and males disperse from their group of birth as they reach adulthood. Among baboons, close relatives do not disperse preferentially to the same group (12, 13). Within each social group, both males and females can readily be ordered in aggression-submission hierarchies in which all adult males rank above the much smaller adult females. Although the female hierarchies are predominantly stable within and even between generations, a male baboon's rank changes frequently, generally peaking in early adulthood (age, 8–10 years) and then declining more or less rapidly (12, 14, 15). Potentially fertile matings occur primarily within close sexual consortships, which involve mate-guarding during days of likely conception. A male can monopolize only a single female when several are simultaneously in estrus.

We first focused on intensive paternity analysis for a cohort of 27 surviving offspring conceived in Lodge Group (7, 16) from 1985 through 1988, a period for which both behavioral and genetic data were available. The time window was then extended both backward 4 years, using only genetic data for 14 surviving offspring, and forward 3 years, using only behavioral data for 42 conceptions (22 surviving offspring), to permit estimation of differential reproductive success for 11 years, approximately the duration of adulthood in this species.

METHODS

Behavioral and Demographic Data. Behavioral studies on Lodge Group began in 1984 (7) and became regular in the next year. Behavioral and reproductive data were collected on all observation days. Reproductive data include each female's reproductive condition (including size and turgescence of sex skin, which in baboons can be used to determine days of likely ovulation to within a few days) and duration of sexual consortships. Agonistic data include records of wins/losses based on aggressive and submissive behaviors, which are used to determine male dominance ranks (17). Because the habitat was open and group size not too large (≈50), both baboons and observers could readily monitor reproductive and agonistic behavior. Because the same observers were monitoring three groups on successive days, however, mating data were available for only a subset of estrus cycles and usually for only one or two of the five most fertile days within any cycle.

Models Predicting Paternity. For 1985–1988, we used behavior to predict paternity in two ways: (*i*) using mating behavior and (*ii*) using the priority-of-access model. For this period, we not only had behavioral and demographic data but we were able to obtain blood samples for 27 offspring as well as for older baboons, including all adult males. To test variability in reproductive success predicted by relative mating behavior, the predicted distribution was determined by using the subset of cycles for which conception occurred and for which we had observed mating behavior on at least one of the fertile days (based on a 5-day fertile period). To test the priority-of-access model, we first determined the frequency of fertile-period overlap among females for the 120 cycles that occurred during 1985–1988. A male can monopolize only one female at a time, and the expected paternity distribution was therefore calculated by assigning paternity solely to the top-ranking male if a conceiving female had no overlap between her fertile days and those of any other female, assigning it

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equally to the top two males when two females overlapped, and so on (2).

Genotyping. Blood samples were collected for the genetic analyses from 76 animals that were immobilized by an anesthetic-bearing dart propelled from a blowpipe (18). The samples included 54 adult females and young from Lodge Group, all adult males from Lodge Group, and 17 additional adult males from other nearby groups; 5 of the 6 males that had been in the group in 1984 when studies began were still there in 1989 and could be sampled. Samples were immediately cooled and within a few hours were spun and frozen for shipping. DNA was extracted from blood as described (19). Genomic DNA was diluted to 1:10 for PCR reactions. Markers included 10 polymorphic microsatellite primer pairs at human map positions D2S141, D4S431, D6S271, D6S311, D7S503, D11S925, D13S159, D16S402, D16S420, and D17S791 (obtained as Human MapPairs from Research Genetics, Huntsville, AL) (20, 21) and transferrin and albumin protein loci (Table 1). The PCR protocol was as follows: the forward (5′) primer of each pair was end-labeled with [γ-^{32}P]ATP using T4-polynucleotide kinase (New England Biolabs) and manufacturer's buffer (70 mM Tris·HCl, pH 7.6). All PCR reactions were carried out in a total of 10 μl containing the following: genomic DNA diluted 1 in 10; 140 μM dNTPs; 10% DMSO; 1 mM MgCl and 0.45 units Taq DNA polymerase with NH_4 buffer [160 mM $(NH_4)_2SO_4$, 670 mM Tris·HCl, pH 8.8 at 25°C, 0.1% Tween-20] with the volume made up to 10 μl with distilled water. PCR amplifications were: one 3-min denaturation at 95°C; 35 cycles of 45 s at 95°C, 1 min at two annealing temperatures (7 cycles at 50°C and 28 cycles at 54°C), and 90 s at 72°C. A 10-min final extension step at 72°C was also included. PCR reactions were carried out in a Hybaid Omnigene thermal cycler. Product (4 μl) was loaded onto 6% denaturing acrylamide gels. The size marker was M13 polycloning site sequence, using adenine and thymine fragments only, loaded in one lane to create a molecular ladder. Gels were exposed to autoradiographic film between 5 hours and 5 days. Genotypes were scored using AT ladder as in ref. 20. Standard starch gel electrophoresis was carried out for allozyme analysis (22).

Parental Analysis. Maternity was determined before genetic work based on observed pregnancies and on observations at or shortly after parturition. For the few infants present at the start of observations, maternity was determined by patterns of suckling and infant care (23). Paternity was determined by cumulative inclusion across 12 loci using the 10 single locus microsatellite markers and 2 serum proteins. Analysis was done for the full set of males regardless of group membership (24). Nonincluded males were excluded on at least two loci, and assigned fathers were included on all loci. Here, we use these paternity determinations solely to examine variability in reproductive success and leave to other reports an investigation of the level of behavioral detail needed for accurate determination of any particular infant's father under various conditions (see *Discussion*).

Relatedness Analysis. In addition to determining paternity through allelic inclusion, we estimated relatedness (R) for each pairwise combination of the 76 sampled individuals using the Queller-Goodnight Index (25, 26). To determine the number of loci needed to provide robust estimates of relatedness, given the variability in our data, we initially selected at random two loci and calculated the R values for all possible pairwise comparisons. We repeated the process by adding one randomly selected locus and calculating R for all pair comparisons at each step until all loci were included. The mean difference in relatedness estimate for different numbers of loci was calculated as the average of absolute differences in R values calculated between steps with n_i and n_{i-1} loci. This procedure was repeated 100 times, providing an estimate of standard deviation. The 10-locus step added only 0.8% change to step 9, and step 12 added 0.6% to the step 11 value.

Table 1. Characteristics of the human microsatellite and protein loci used in this study

Locus (human map position)	Allele	Frequency
D2S141	128	0.81
	130	0.19
D4S431	212	0.03
	214	0.74
	216	0.23
D6S271	166	0.08
	168	0.39
	172	0.36
	182	0.08
	186	0.02
	190	0.04
	198	0.03
D6S311	228	0.65
	230	0.11
	232	0.11
	234	0.13
D7S503	156	0.42
	158	0.06
	160	0.02
	164	0.02
	166	0.05
	170	0.35
	172	0.08
D11S925	194	0.45
	196	0.35
	198	0.20
D13S159	164	0.12
	168	0.22
	170	0.16
	172	0.45
	180	0.05
D16S402	144	0.03
	146	0.31
	150	0.24
	154	0.24
	164	0.07
	170	0.11
D16S420	194	0.04
	196	0.23
	198	0.67
	200	0.06
D17S791	166	0.06
	168	0.03
	170	0.06
	172	0.26
	174	0.42
	176	0.10
	182	0.05
	184	0.02
Transferrin	s	0.39
	m	0.52
	f	0.09
Albumin	s	0.09
	m	0.91

For microsatellites, allele numbers represent the size in base pairs of the PCR product, measured relative to M13 ladder. For protein alleles: s, slow migrating allele; m, medium allele; and f, fast allele.

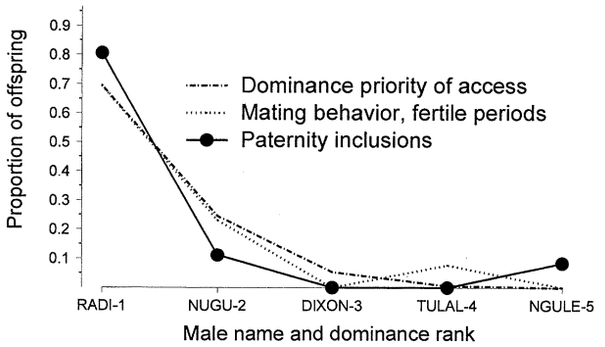

FIG. 1. The close relationship between socially predicted and genetically identified paternity for males of each dominance rank, 1985 through 1988 (χ^2 test, $P > 0.05$ for both dominance-based and behavior-based models). Paternity assignment was carried out by allelic exclusion analysis across 12 loci (see text). If blood was available for the mother, hers as well as the offspring's genotype was considered in making paternity exclusions. Excluded males failed to match with potential offspring on at least two loci. [Exclusion probabilities (24) averaged 0.904, median 0.928.]

RESULTS

The paternity distribution for 1985-1988 (Fig. 1) provides strong support both for the dominance-based priority-of-access model and for the validity of estimating variance in reproductive success using consortships on fertile days of conception cycles. The top-ranking male, Radi, fathered 81% of the 27 surviving offspring during this 4-year period, and most of the offspring produced during this period were, therefore, related at least at the level of (paternal) half-siblings (27, 28).

To evaluate long-term patterns of reproductive success, we first extended the time window backward and examined whether the 1985–1988 pattern of paternity variability pertained for conceptions during the several years before observations. Paternity exclusions for 14 surviving offspring conceived from 1981–1984 identified Radi as the only included male for 6 of the 14 juveniles, but Radi was excluded for the other 8. The second-, third-, and fourth-ranking males of 1985–88 were each assigned one offspring from the earlier cohort. All sampled males were excluded as fathers for the remaining five offspring, and at most three of the five could have had the same father. Overall, the pattern of age cohorts as paternal sibships that pertained in 1985–1988 was also apparent for the previous 4 years in that a single, unidentified male was implicated as the father for the three oldest juveniles, and Radi as the father for six of the nine youngest ones. Nonetheless, no single male retained reproductive monopoly over the full 4-year period—none could have fathered more than 43% of the offspring.

Next, we extended the time window forward for conceptions after 1988 by estimating variability in reproductive success during 1989–1991 from both priority-of access and observed mating behavior (most offspring from these later cohorts were not yet large enough to dart when we collected blood samples).

In contrast to 1985–1988, during the next several years, a number of rank changes occurred among the adult males and no single male retained high rank continuously for more than a year. Moreover, the top-ranking position was often occupied by young males who had mothers and/or maternal sisters among the adult females, and consortships did not occur among such close relatives (see also ref. 13). Nonetheless, mating success remained highly skewed and the distribution of mating success remained well-predicted by the dominance-based priority model (Fig. 2). The correlation between the estimated paternity distribution among individual males based on priority-of-access and that based on observed mating

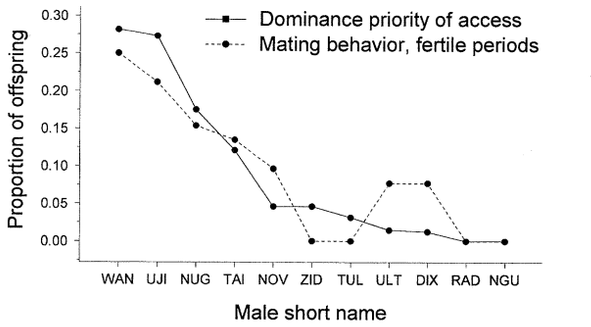

FIG. 2. Variability in estimated reproductive success for potential fathers of the 40 offspring that were conceived 1989-1991. Estimation is based on two behavioral models, dominance-based priority-of-access and mating behavior during the fertile periods of the conceptive cycles (as in Fig. 1), which were highly correlated ($r = 0.92$). Shortened (three letter) names are given for each male who was an adult in the group any time during this period. Because male dominance rank changed frequently during these 3 years, no simple listing by rank, as done in Fig. 1, could be done for these years as a whole; rather, males are listed according to a close equivalent, their order based on the dominance-priority model. The adult males present here but not in Fig. 1 are younger males that matured subsequently. Uji, Nugu, and Wang each spent some time at the top rank position; the previous top-ranking male, Radi, was consistently low-ranking after 1988. Tulal and Ngule died near the end of 1989.

behavior, although not as high as it had been during the longer period of stability ($r = 0.99$), was still quite high ($r = 0.92$). Consequently, we use relative mating success as a preliminary estimate of relative reproductive success for 1989-1991 in the analyses for the whole time span 1981–1991.

In considering the full 11 years covered by our three-stage analysis, even Radi, who had high mating success for an unusually long period of at least 4 out of 11 years and fathered 81% of the offspring during his years as top-ranking male, fathered only an estimated 44% of the 63 surviving offspring conceived during the full 11 years, approximately the average duration of adulthood. His offspring production was three times that of any other male over that total period, but his proportional share was only a little over half the proportion that he achieved during the years that he was high ranking.

Both a male's adult tenure and his per annum production of offspring contribute to his long-term production of offspring. For the 20 males that were adults in the group during some portion of the 7-year period, 1984–1991 (the period for which we know the identity of all males), tenure as adults in the group during this period ranged from less than 1 year for nine males to the full 7 years for three others (Radi, Nugu, and Dixon). Estimated per annum production of surviving offspring for the 11 with tenure of least a year ranged from 0 for Tulal and Zidi, to 3.14 for Radi ($\bar{x} = 0.85$, SD = 0.96). Radi's rate was double that of Uji and Nova, whose rates were double those of Tai and Ultra; the remaining five males were estimated to have fathered less than a half offspring per annum. The nine males with tenure less than a year all had paternity estimates of zero surviving offspring and left the group without having had sexual consortships during females' fertile periods (see also refs. 13 and 14).

The final genetic analysis was conducted to examine the predictions provided by dispersal-based models for genetic structure within the group as a whole. Having determined that the 12 loci provided stable measures of relatedness using the Queller-Goodnight Index (see *Methods*), we then calculated pairwise relatedness using the 12 loci, and we grouped pairs of individuals to test the predicted ordering of relatedness classes based on the prior determinations of maternity and paternity and on the matrilocal, male-dispersing social system.

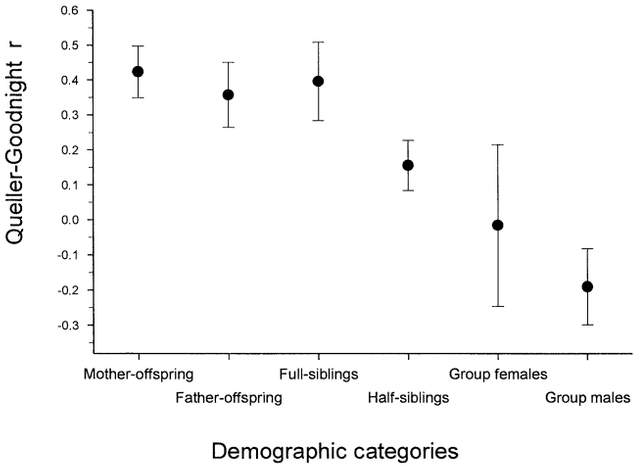

FIG. 3. Mean pairwise relatedness values for pairs of individuals in different categories (25). The first three categories are first-degree relatives which should have equal values of R (however, variability in R is expected to be greater for the sibling class than for the parent-offspring classes). R for half-siblings is expected to be half that for first-degree relatives. Mother-offspring and father-offspring pairs were identified as indicated in the text. Full-sibling pairs were those that shared both mother and father. Included as half-siblings were either maternal siblings who were determined to have different fathers, paternal siblings who did not have the same mother, or maternal siblings for whom we do not know whether they have the same father (as a consequence, these may include a few pairs of full-siblings). Group adult females and males are those identified as initial, presumed unrelated adults when studies began. Note that absolute relatedness estimates for all categories were slightly below expectation due to the high background relatedness in the sample used. SEs for each category of individuals were calculated by first averaging jackknife values over all pair comparisons within a class for each of the 12 loci. The end result was 12 mean values that were used as the initial values for the SE calculation (29).

Clear support for each prediction was provided by the genetic relatedness values in the group (Fig. 3). On average, pairs of adult males were less closely related than were pairs of adult females. Mother-offspring pairs, father-offspring and full-sibling pairs (using paternity assignments as described above), were the most closely related and had values approximately double that among half-siblings. For adult-youngster pairs in the group, relatedness values among adult female-juvenile pairs were higher than that among adult male-juvenile pairs, as expected if the set of mothers is more closely related than is the set of fathers. Finally, for nine initial matrilines in Lodge Group, relatedness was greater within matrilines than between matrilines.

DISCUSSION

Variance in short-term reproductive success was high for all three time blocks of our study, for the first period using only genetic data, for the second both genetic and behavioral data, and for the third using solely behavioral data. Moreover, for the 7-year period in which dominance status was known, dominance-based priority-of-access provided the main source of the variance among males. This finding is consistent with those of the two other genetic studies of wild primates (30, 31). As a result, the period over which any particular male experienced high success was a function of the length of time in which he was high-ranking (30).

Although not evidenced in our data, several factors may influence the strength of the relationship of dominance to mating success, mating success to reproductive success, and hence, dominance to reproductive success in primate groups (32–35). Therefore, these factors will affect the generality of our results. First, certain ecological conditions in the wild can limit a dominant male's ability to exercise priority without intolerably compromising foraging or rank-maintenance activities while mate-guarding during consortships (36). These limitations will arise when groups are very large, when dominance ranks are unstable or rates of immigration are high, when habitats have many visual obstructions, or when foraging demands are high. Second, differences among males in their social relationships with other members of the group can lead to success of male-male coalitions against dominant males or to nondominance-based female choice. Either situation would reduce dominance-based mating success (37–41). Finally, at least for macaques, conditions of captivity may partially account for the relative lack of dominance priority found in studies of captive colonies compared with those of wild populations (35).

In any of the conditions in which dominance priority is at least partially offset by other factors, estrous females are likely to have more different mates because no single male, dominant or otherwise, will monopolize a female throughout her fertile period. From the standpoint of males, a premium is put on efficient identification of the most fertile females and the most likely times of conception. General mating success does not necessarily translate into success in producing surviving offspring, which is what is measured in paternity determinations. Factors that may either reinforce or counteract differential mating success include variability in fertility among both males and females, sperm selection/competition, variability in ability to maintain a pregnancy, and differences in offspring survival that may arise from either parent, but will in general be more affected by the parent that provides more offspring care. Apparent differences between variability as measured by mating success and variability as measure by paternity of surviving offspring may reflect inadequacies of the behavioral data that are used (42–44). These differences may arise at least partially, however, through selection processes other than differential mating success.

Finally, the contrast between short-term and long-term reproductive success has several implications. Lifetime reproductive success cannot in general be deduced from short-term measures of reproductive success. More males will contribute to the gene pool than predicted from highly skewed short-term reproductive success, resulting in greater effective population size. Age cohorts will to a considerable extent represent separate paternal sibships (26, 27), and a group's genetic composition will vary appreciably, both over time and among age classes at any one time. Temporal patterns of genetic stability and instability, and the lifetime differences in male reproductive success that they reflect, have potentially important implications for the evolution of social behavior. Their evaluation requires long-term studies of natural populations.

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