

Environmental and genetic causes of maturational differences among rhesus macaque matriline

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Abstract Females of many cercopithecine primates live in stable dominance hierarchies that create long-term asymmetries among sets of female relatives (matrilines) in access to limiting resources and shelter from psychosocial stress. Rank-related differences in fitness components are widely documented, but their causes are unclear. Predicted breeding values from an animal model for female age of first reproduction are used to discriminate between shared additive genetic and shared environmental effects among the members of matriline in a population of free-ranging rhesus macaques (*Macaca mulatta*). While age of first reproduction has a modest heritability (≈ 0.2), breeding values are distributed in a largely random fashion among matriline and contribute little to the observed rank-related differences in average age of first reproduction. These results support the long-held, but previously unverified, contention that rank-related life history differences in female cercopithecine primates are the result of environmental rather than genetic differences among them.

Keywords Social dominance · Breeding value · Quantitative genetics · Heritability · Female maturation · Cayo Santiago

Introduction

Any phenotype emerges from the interaction of genes and environments (Templeton 2006; West-Eberhard 2003). In social animals with extended parental care, such as primates, there are opportunities for social transmission of phenotypic effects along and across kin lines that make these gene–environment interactions multigenerational (Rossiter 1996; Wolf et al. 1998; Laland et al. 2000; Silk 2002). Patterns of social dominance among many species of female cercopithecine primates are a simple model system in which to study the effects of these parallel pathways of social and genetic inheritance on important phenotypic outcomes that are likely to have effects on lifetime fitness. Intergenerationally consistent patterns of unequal environment quality are potentially important in structuring how traits experience selection in heterogeneous populations (Pettay et al. 2007; Wilson et al. 2006).

Social dominance for females of many macaque species (*Macaca*) follows a clear set of rules whereby daughters occupy a rank in the dominance hierarchy just below their mother and are followed by each of their older sisters (Kawai 1965; Sade 1967; Thierry et al. 2004). These sets of adjacent-ranking female kin that are all descended from a crown female ancestor are called matriline. Because matriline members are generally adjacent to one another, forming blocks within the group dominance hierarchy, the rank of entire matriline can be used as a proxy for individual rank in social groups containing multiple matriline (Bercovitch and Berard 1993; Stucki et al. 1991).

The formation of cooperative coalitions within matriline is instrumental in maintaining and acquiring rank (Chapais 2004; Datta and Beauchamp 1991),

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behaviors that have largely been explained through kin selection (Silk 2002; Chapais 2001). Rank affects health by providing priority of access to limited resources (Koenig 2002) and shelter from stress induced by aggressive interactions (Sapolsky 2005). Because females remain in their natal group for life and the matriline dominance relationships are stable, rank may affect many variables throughout the life course. In wild and free-ranging macaques, baboons (*Papio*), and vervets (*Cercopithecus*), high-ranking females frequently mature earlier, have higher infant survival rates, and give birth to surviving infants over shorter time intervals than their lower-ranking peers (Whitten 1983; Harcourt 1987; Stucki et al. 1991; Bercovitch and Berard 1993; Ellis 1995; van Noordwijk and van Schaik 1999; Packer et al. 1995; Altmann et al. 1988).

These phenotypic comparisons suffer from an important shortcoming. Because matriline members have similar ranks within a social group's dominance hierarchy and are also genetically related, and because many mammalian life history traits are known to be heritable, it is unclear to what extent the environment provided by social rank or potential genetic differences among matriline members contributes to these regularly observed life history disparities (Silk 1984). Genetic and rank-related environmental differences are confounded in simple phenotypic comparisons. However, techniques used by animal breeders can be applied to resolve this question by separating genetic and environmental contributions to phenotypes of pedigree members (Postma 2006; Postma and Charmantier 2007). This requires paternal genealogical links or cases of change in female rank, both of which provide genetic linkages between rank environments. The resulting predicted breeding value (PBV) is an estimate of the additive genetic value of an individual for a given trait, or how much the alleles an individual carries cause it to depart from the population mean for the trait (Kruuk 2004; Mrode 1996).

Female age of first reproduction (AFR) is particularly amenable to this quantitative genetic approach. It is easily quantified and can be measured on many more individuals than lifespan, birth rate, or lifetime reproductive output in most primate populations (Kappeler and Pereira 2003). Estimates for heritability of AFR are also typically larger than zero, suggesting substantial genetic variation (Blomquist 2009; Towne et al. 2005; Williams-Blangero and Blangero 1995). Furthermore, previous research has shown social rank strongly influences AFR in many female primates (Ellis 1995). Finally, variation in AFR is theoretically important in

models of population growth and evolutionary genetics (Charlesworth 1994).

Methods

I examined female AFR in a large population of free-ranging rhesus macaques (*Macaca mulatta*) that were transplanted to the 15.2-ha island of Cayo Santiago, Puerto Rico, from India in 1938. Monkeys are fed commercial monkey chow and provided water ad libitum, but they forage on natural vegetation and live in naturally formed social groups (Rawlins and Kessler 1986). At the time of the study in 2005, there were 7,938 known individuals who had lived on the island.

Three increasingly limited subsets of this full data set were used in the analysis. First, data were limited to a single, large interlocking pedigree of 6,543 individuals in 17 matriline linked by paternities. Paternities were determined by microsatellite variation (Nurnberg et al. 1998). This pedigree comprises 82% of the full database and includes nine generations of monkeys. Maternal sibships range from zero to 18, while paternal sibships range from zero to 28. Pedigree membership and sibship size were identified from the database using PEDSYS (Dyke 1996). Focusing the analysis on this pedigree ensures all maturing females will have relatives that contribute information to their breeding values (see explanation of pedigree connectedness and trait reliability below).

Second, AFR data for members of this pedigree were limited to females born between 1960 and 1996 such that they had been reliably aged and placed in a matriline rank category. Rhesus macaques are seasonal breeders and usually bear their first offspring in the third to sixth annual cycle after they were born. Any individuals with AFR outside this age range were excluded from the analysis ($n = 3$). This yielded a total of 847 records of AFR. This subset of records was only used for estimating variance components and heritability of AFR.

Finally, phenotypic tests for rank-related differences in AFR and prediction of breeding values were carried out with a smaller data set of 674 records of AFR corresponding to a later time period (1975–1996 birth cohorts) when most social groups consisted of two to four matriline. This allowed matriline rank to be scored as a three-level ordinal variable (high, middle, low) based on behavioral records of pairwise agonistic encounters between individuals over the first 4 years of

life (provided by D. S. Sade and J. D. Berard). In cases where a social group had two matriline, they were scored as high and low. If there were four matriline, the two middle-ranking matriline were both scored as middle. Females in groups with only one matriline were excluded from analysis. Prior to this period, groups consisted of many matriline such that breaks between the three ordinal rank categories were much more arbitrary.

Previous research on female maturation at Cayo Santiago has demonstrated phenotypic shifts toward later maturation that likely correspond to rising population density (Bercovitch and Berard 1993; Stucki et al. 1991). Because of these differences, I separated the 1975–1996 time span into two periods—one of lower (1975–1984; $\bar{x} = 681.70$, $SD = 268.06$) and one of higher (1985–1996; $\bar{x} = 996.00$, $SD = 212.89$) density (Table 1). I tested the association between matriline rank and AFR with the Spearman rank correlation on the individual records of rank and AFR (r_s , Kendall 1948).

Age differences within birth cohorts complicate interpreting these correlations because females born late in their cohort may be less likely to have first birth in a year than the older members of the same cohort. To account for this, a general linear model was used to predict AFR by their matriline rank and a covariate

that measured age within a birth cohort. The covariate was the number of days after the beginning of the annual birth season (set as September 1) that a female was born. The vast majority of births (90%) occur between December and April (Rawlins and Kessler 1985; Blomquist 2007). Correlation and general linear models were run in R Development Core Team (2007). Linear contrasts were used to test for mean differences between pairs of rank categories from the general linear model.

An “animal model” was used to estimate variance components and predict breeding values for AFR, as implemented in the software VCE 5.1 and PEST 4.2 (Groeneveld and Kovac 1990). Data on the 847 females born between 1960 and 1996 were used in estimating variance components and predicting breeding values, but only the breeding values from 1975 to 1996 were used for comparison with the phenotypic data. The animal model is a mixed linear model (Eq. 1), where \mathbf{y} is a vector of phenotypic data, \mathbf{X} is a design matrix for fixed effects, \mathbf{b} is a vector of fixed effects used for controlling known variation among individuals, \mathbf{Z} is a design matrix for random effects, \mathbf{a} is a vector of random effects including the individual breeding values, and \mathbf{e} is the residual error (Kruuk 2004; Lynch and Walsh 1998).

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \quad (1)$$

The model used in estimating variance components included the fixed effect of matriline rank, a three-level fixed factor indicating the time period in which a female was born (1960–1974, 1975–1984, or 1985–1996), and a covariate for when during the birth season a female was born to correct for age differences among females within annual cohorts. The same fixed factors were used for predicting breeding values, except that rank and time period were entered as an interaction. The only random effect was the additive genetic breeding value. Using this model, the phenotypic variance after fixed effects are accounted for is the sum of additive genetic and residual variance ($V_P = V_A + V_E$). The total phenotypic variance will be larger than this and include variation attributed to fixed effects (Wilson 2008). This provides two estimates of the narrow sense heritability ($h^2 = V_A / V_P$) of the trait: h^2_A uses the phenotypic variance after fixed effects are removed, and h^2_T uses the total phenotypic variance including that due to fixed effects. Wilson (2008) proposed that h^2_T is better for comparisons among published heritability estimates because it does not depend on the fixed effects used in the animal model.

Table 1 Phenotypic distribution of female AFR by matriline rank and time period at Cayo Santiago

Rank	AFR				Row <i>n</i>
	3	4	5	6	
1975–1996 birth cohorts					
High	5.1	73.0	20.7	1.2	256
Middle	1.8	66.8	28.3	3.1	226
Low	0.5	68.2	25.5	5.7	192
$r_s = 0.123$, $p = 0.001$					
1975–1984 birth cohorts					
High	7.5	73.3	19.2	0	146
Middle	2.7	81.3	14.7	1.3	75
Low	0	83.0	15.0	2.0	100
$r_s = 0.045$, $p = 0.421$					
1985–1996 birth cohorts					
High	1.8	72.7	22.7	2.7	110
Middle	1.3	59.6	35.1	4.0	151
Low	1.1	52.2	37.0	9.8	92
$r_s = 0.177$, $p < 0.001$					

Values are reported as row percentages along with the row total. A Spearman rank correlation (r_s) on the raw data tests for an association between rank and female AFR

Postma (2006) has argued that exploration of breeding values must be done with a full understanding of the reliability of PBVs and clear statement of null hypotheses when testing for trends within them. When individuals are not randomized among environments, a PBV is not equivalent to the true breeding values and will continue to reflect the environmental component of an individual's phenotype. Reliability (r^2) is a measure of how well PBVs reflect true breeding values. Technically, reliability indicates how much information is contributed to breeding values by records on related individuals beyond the individual's own phenotype and the trait heritability. It is calculated as the ratio of the variance in the PBVs to the additive genetic variance ($r^2 = V_{PBV}/V_A$). The range of the reliability spans from the heritability, where relatives contribute nothing to the breeding values, to one, where predicted values are equivalent to true breeding values. Reliabilities much larger than heritabilities indicate that the PBVs are accurate reflections of the true breeding value.

Once generated, PBVs can be analyzed like phenotypic data using standard statistical software (Kruuk 2004). Interpretation of trends in the breeding values depends on the quality of the pedigrees used (Postma 2006; Postma and Charmantier 2007). Small numbers of pedigree links across rank categories, a situation known as low connectedness (Kennedy and Trus 1993), will cause low trait reliability and limit power for detecting or rejecting trends in the PBVs. To demonstrate that AFR records in the Cayo Santiago pedigree are well-connected, I calculated the percentage of close relatives (coefficient of relationship ≥ 0.125) maturing in matriline rank categories different from the rank category of each individual (Garant et al. 2005). Pairwise coefficients of relationship were determined by the Stevens–Boyce algorithm implemented in PEDSYS (Boyce 1983; Dyke 1996).

Results

Phenotypic rank-related trends

There are consistent phenotypic differences in AFR among high-, middle-, and low-ranking matrilines at Cayo Santiago (Stucki et al. 1991; Bercovitch and Berard 1993). Of females born between 1975 and 1996, higher-ranking females matured earlier than those of lower rank (Table 1; $r_s = 0.123$, $p = 0.001$). However, this trend was only significant in the later time period of higher density, from 1985 to 1996 ($r_s = 0.177$, $p < 0.001$).

The general linear model for AFR shows the expected delay in AFR with a drop in rank (Fig. 1a) when adjusting for age differences within birth cohorts. However, the difference is only significant in the higher-density 1985-to-1996 period (model $R^2 = 0.10$, $F_{6,667} = 12.17$, $p < 0.001$; linear contrasts for rank in 1975–1984 $p = 0.724$, and rank in 1985–1996 $p = 0.012$).

Heritability of female AFR

AFR has a small heritability, but it is significantly greater than zero ($h_A^2 = \frac{0.066}{0.306} = 0.217$, SE = 0.048; $z = 4.55$, $p < 0.001$). The total heritability is only slightly lower ($h_T^2 = \frac{0.066}{0.326} = 0.204$) than this estimate. Both values are consistent with other maturation heritabilities for this population (Blomquist 2007, 2009). The small

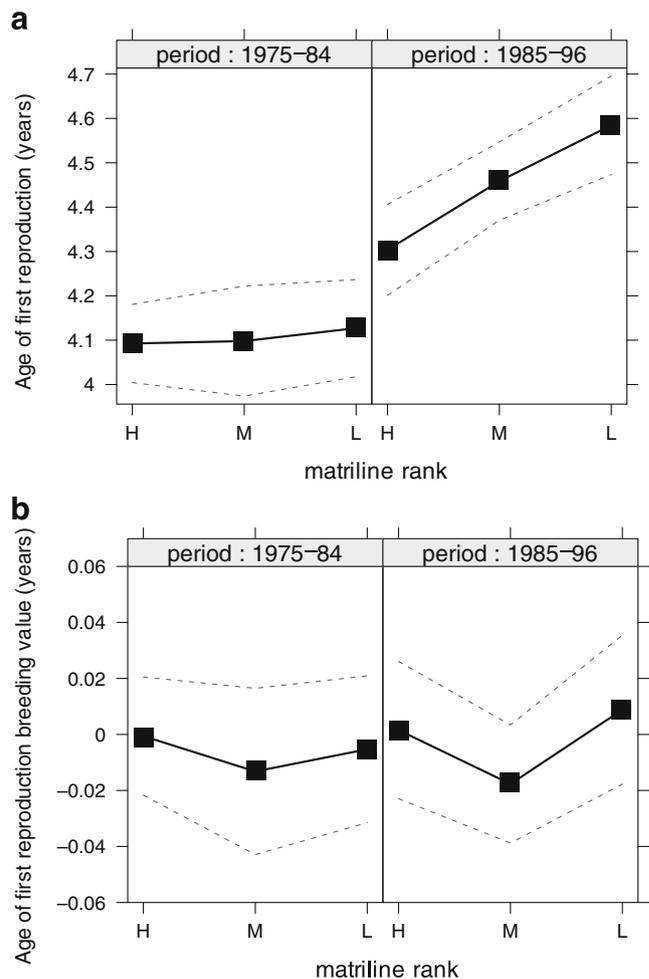


Fig. 1 **a** Adjusted phenotypic, and **b** PBV means and 95% confidence intervals for female AFR at Cayo Santiago by matriline rank and time period. Corresponding general linear models used female birth date, time period, and matriline rank to predict the dependent variable. See text for significance tests

difference in the denominators of these two heritability estimates indicates the variance accounted for by the model fixed effects (age within birth cohort, matriline rank, and time period) is relatively small. This “fixed effects variance” is approximately 6% of the total ($\frac{0.326-0.306}{0.326}$). The remaining 74% of the phenotypic variance is unexplained residual.

Trait reliability and pedigree connectedness

The reliability for AFR is about 10% larger than the heritability ($r^2 = 0.245$). Furthermore, in the 1985–1996 period, where the bulk of the paternities are confined, the reliability is substantially higher ($r^2 = 0.310$).

Most females in the data set have about 20% of their close relatives (coefficient of relatedness ≥ 0.125) in rank categories other than their own (Table 2). Consequently, tests for trends in PBVs from an animal model that included rank should be able to detect remaining trends in the PBVs.

Absence of rank-related trends in breeding values

In contrast to the phenotypic pattern, a general linear model identifies no rank-related trends in the PBVs (model $F_{6,667} = 1.10$, $p = 0.365$; linear contrasts for rank in 1975–1984 $p = 0.688$, and rank in 1985–1996 $p = 0.408$). Small differences in rank category averages may enhance or reduce the much larger phenotypic differences in the 1985-to-1996 period, though none of them are significant (Fig. 1b). During this period, the difference in average breeding value for high- and middle-ranking females is in the opposite direction of the phenotypic data (0.019 years, contrast $p = 0.234$). That between low- and middle-ranking females matches the phenotypic trend (0.027 years, $p = 0.120$). Regardless of the significance of the differences among breeding value means, they are small compared to the phenotypic differences among rank categories in this period ($\leq 21\%$).

Table 2 Distribution of pairs of maturing females among high, middle, and low matriline rank categories for which the coefficient of relationship ≥ 0.125

	High	Middle	Low	% Different
High	1,048	240	52	21.8
Middle		1,264	121	22.2
Low			609	22.1

Discussion

The results of this analysis support the long-held, but previously unverified, contention that rank-related matriline life history differences in female cercopithecine primates are the result of environmental rather than genetic differences among them (Silk 1984; Altmann et al. 1988; Stucki et al. 1991; Bercovitch and Berard 1993; Packer et al. 1995; van Noordwijk and van Schaik 1999). This is encouraging for workers in the field who may never have access to rich genealogical or genetic information on their study populations but can document the environmental factors that cause rank to influence life history traits by predicting priority of access to limited resources and shelter from stress (Koenig 2002; Sapolsky 2005). Detailed information on wild baboons also supports the view that female maturation is heavily influenced by the environment experienced by and provided by maternal kin, whereas these kin or maternal effects are weak on males (Altmann and Alberts 2005; Charpentier et al. 2008). In this baboon population, it was components of the social environment—mother’s presence, mother’s rank, number of maternal half-sisters, and number of mature females—that were useful predictors of infant growth rates and age of female maturation.

Early life traits, such as growth rates or age of maturation, are the most common to be influenced by maternal effects (Rossiter 1996; Cheverud and Moore 1994; Altmann and Alberts 2005). Recent perspectives on maternal effects have emphasized the likelihood of developmental plasticity evolving when the maternal phenotype or environment is a reliable predictor of offspring environment (Uller 2008; Galloway and Etterson 2007), especially when environments are highly heterogeneous (Pigliucci 2001). Inheritance of these environmental effects may occur through parental nutrition, hormonal signals, pathogen or toxin exposure, and behavioral conditioning that affect offspring during prenatal or postnatal life (Rossiter 1996).

Female AFR is an outcome dependent on these factors, some of which are known to correlate with matriline rank and likely act at multiple points during infant and juvenile development. Importantly, there are consistent differences among mothers in their style of infant care that tend to match maternal rank and influence the scope of group members and variety of interactions infants experience (Altmann 1980; Berman 1983; Chauvin and Berman 2004). Furthermore, consistency of cross-fostered captive rhesus macaque offspring aggressive and contact behaviors with their birth mothers points to prenatal sources of variation, or possibly even direct genetic effects on the behaviors

(Maestriperieri 2003). Nevertheless, macaque molecular genetic studies also implicate sensitivity to rearing and social conditions in producing aggressive phenotypes that may affect rank acquisition or maintenance (Canli and Lesch 2007).

The heritability estimate for AFR for the Cayo Santiago females differs from the only previous estimate for a non-human primate population. It is much higher in captive baboons, which live in a much more controlled environment ($h^2 = 0.87$, Williams-Blangero and Blangero 1995). Heritability studies on living and historical human populations indicate a wide range of values can be found for menarcheal age and AFR (Towne et al. 2005; Pettay et al. 2005; Kirk et al. 2001). This suggests that these are largely population-level rather than interspecific differences. Heritabilities of life history traits such as AFR are generally expected to be low either because past selection has eroded additive genetic variation (Roff and Mousseau 1987) or because there are more physiological and environmental factors that determine life history traits than morphology—increasing their residual variation (Price and Schluter 1991). A low heritability of ≈ 0.2 for AFR at Cayo Santiago is unsurprising. Additional sources of variation will be contained in the residual variance (V_E) for AFR. These include genetic dominance and epistasis and other environmental factors beyond matriline rank and time period as they were used in the animal model. Individual rank differences within matriline may also explain some variance but were not available for this study.

The lack of breeding value differences among rank categories also implies some aspects of the evolutionary dynamics of female AFR in this population. Because breeding values are essentially randomly distributed among rank categories, predicting response to selection will not be complicated by gene–environment covariance (van Tienderen and de Jong 1994). Furthermore, the accurate prediction of response requires an estimate of the heritability that is unpolluted by shared environments among relatives; this is provided by the animal model (Kruuk 2004). Nevertheless, selection on AFR in female primates is likely complex, involving trade-offs with infant survival and maternal survival or future reproduction (Bercovitch et al. 1998, 2000; Bercovitch and Berard 1993) that may be genetically correlated and strongly influence evolutionary response (Stearns 1989; Pettay et al. 2005; Blomquist 2007).

Finally, it is worth noting that, despite the large environmental contribution of rank to phenotypic differences in AFR, selection on it is not strictly on the environmental component of phenotypic variation (Kruuk et al. 2002, 2003; Price and Schluter 1991).

The random distribution of breeding values suggests they will be subject to selection via their rank-related component and can provide an adaptive response. In other words, the environmental variation associated with rank (e.g., nutrition, stress) will not complicate the evolutionary dynamics of AFR because it is uncorrelated with genetic variation for this trait (van Tienderen and de Jong 1994). This is a legitimate assumption for the evolutionary dynamics of other life history variables influenced by rank but should be tested when possible.

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