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Chapter 9

Female Age of First Reproduction at Cayo Santiago: Heritability and Shared Environments

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9.1 Introduction

The timing of female sexual maturation or age of first reproduction (AFR) is one of the most frequently studied life history variables by primatologists (Kappeler and Pereira 2003; Charnov and Berrigan 1993; Ross 1988). Within population variation in AFR has been a particular focus of research on the fitness benefits and costs of social status in cercopithecine primates (especially macaques, baboons, and vervets) with strong, stable dominance hierarchies and female philopatry (Whitten 1983; Harcourt 1987; Silk 1987; Altmann et al. 1988; Cheney et al. 1988; Sade 1990; Stucki et al. 1991; Bercovitch and Berard 1993; Ellis 1995; Packer et al. 1995; van Noordwijk and van Schaik 1999). Female philopatry is important because the formation of cooperative coalitions within matriline (sets of females descended from a single founding female ancestor) is instrumental in maintaining and acquiring rank (Chapais 2004; Datta and Beauchamp 1991; Datta 1983a, b). Rank affects health by providing priority of access to limited resources (Koenig 2002) and shelter from stress induced by aggressive interactions (Sapolsky 2005). Females of higher rank tend to have earlier AFR which, all things being equal, provides a fitness advantage (Stearns 1992; Sibly and Calow 1986).

Pioneering research on Cayo Santiago macaques provided some of the earliest demonstrations of rank-related life history benefits for female primates (Drickamer 1974; Sade et al. 1976), and unraveled the typical patterning of social dominance in rhesus macaques and their closest relatives within the genus (Sade 1967; Missakian 1972; Kawai 1965; Kawamura 1965; Thierry et al. 2004). Females form a linear dominance hierarchy with daughters ranked just below their mothers. As younger

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sisters reach maturity, they displace their older sisters and occupy the rank immediately below their mother (Schulmann and Chapis 1980). Matriline members thus form blocks within the dominance hierarchy of roughly similar status.

This chapter builds on this remarkable foundation of research to present the results of several quantitative genetic studies on phenotypic variation in AFR at Cayo Santiago. Previous quantitative genetic work with the Cayo Santiago macaques primarily dealt with morphology (e.g., Cheverud 1981, 1982; Cheverud and Buikstra 1981a, b; McGrath et al. 1984; Cheverud et al. 1990; Hallgrímsson et al. 2002). There remains relatively little published quantitative genetic information on the life history traits of non-human primates (Martin et al. 2002; Jaquish et al. 1996; Williams-Blangero and Blangero 1995; Cheverud et al. 1994). Though developed by animal breeders (Kruuk 2004; Lynch and Walsh 1998; Postma 2006), the methods of quantitative genetics are increasingly being employed to answer questions about variation in wild and free-ranging populations, such as "How much of the variation in AFR is due to genetic variation?" and "Do high ranking females mature earlier because they share a common beneficial environment or because they have genes that promote more rapid maturation than their lower-ranking peers?"

9.1.1 Genetic, Cohort, and Maternal Effects

In this chapter, I use quantitative genetic methods to address two major questions about female AFR at Cayo Santiago. The first involves the estimation of underlying variance components that contribute to the phenotypic variation in AFR. I explore three main sources: additive genetics, cohort effects, and maternal effects. Additive genetic variance is that due to differences among population members in their breeding values. Breeding values can be thought of as a multilocus genotype for AFR, or how much the alleles an individual carries causes it to depart from the population mean for AFR. Additive genetic variation for a trait is often reported as a heritability, the ratio of additive to phenotypic variance ($h^2 = V_A/V_P$). Because relatives share genes according to the rules of Mendelian inheritance, the resemblance among relatives can be used to separate this genetic source of variation from environmental causes (Lynch and Walsh 1998). Cohort effects are the result of temporal variation in a variety of factors that may affect AFR, such as group or total population density, food abundance, or disease prevalence. Animals born in the same cohort are likely to be more similar to one another because of these shared aspects of their environment. Finally, maternal effects are caused by offspring sharing the special, intimate environment provided by their mothers, pre- and postnatally (Maestriperieri and Mateo 2009; Cheverud and Wolf 2009; Wolf and Wade 2009).

Maternal effects have received increased attention from primatologists, often focused on the intergenerational transmission of behavior. Because mothers transmit their social rank as well as their genes to offspring, the patterning of social dominance in female macaques has been explained as a possible maternal effect on offspring life history traits (e.g., Maestriperieri 2009; Charpentier et al. 2008; Altmann and Alberts 2005; Setchell et al. 2001; Hrdy 1999). High-ranking females are born

with a "silver spoon" of a benign social environment while lower-ranked females have to make the best of their bad situation (Grafen 1988). Such studies use a straightforward route to identify maternal effects either by exploiting variation among the offspring of a single female and relating it to some known difference among the offspring (e.g. birth order) or comparing the offspring of different mothers and relating outcomes to a measurable maternal characteristic (e.g., dominance rank). For example, Altmann and Alberts (2005) found higher-ranking baboons at Amboseli had offspring that were relatively larger for offspring age, and primiparous mothers had relatively smaller juveniles. Similar birth order effects have also been documented in captive macaques (Broadhurst and Jinks 1965).

An alternative approach borrowed from animal breeders (Wilham 1963; Bijma 2006) that has been used successfully with wild populations of birds and mammals is the estimation of a maternal variance component (V_M) or maternal effect ($m = V_M/V_P$) within a quantitative genetic model (Kruuk and Hadfield 2007; Kruuk 2004; Kruuk et al. 2000; Wilson et al. 2005; Keller et al. 2001; Cheverud and Moore 1994). This is identical to household effects identified in studies of humans (e.g., Pettay et al. 2005; Towne et al. 2005). For example, Kruuk et al. (2000) found that birth weight in female red deer had a maternal effect of about 0.20 and the heritability of 0.25, meaning that the identity of a mother (a proxy for the environment she provides) explained an additional 20% of phenotypic variation beyond the additive genetic effects gauged by the heritability. This quantitative genetic method only partially overlaps with the phenotypic approaches discussed earlier. For example, the rank effects on baboon mass could contribute to m , but the primiparity effect on mass would reduce m because it causes offspring of the same female to differ from one another. The analysis presented in this chapter is intended to help clarify the influence of maternal effects on primate life histories by taking both approaches to unpack variation in female AFR at Cayo Santiago – identifying maternal characteristics that influence AFR similar to Altmann and Alberts (2005) through phenotypic regressions and deploying quantitative genetic techniques to estimate m .

9.1.2 Rank-Related Trends in AFR: Genes or Environment?

The second major topic of this chapter is highlighting and providing a tentative answer to an often-overlooked problem in comparing the life history traits of female macaques of different rank. Strictly phenotypic comparisons suffer from an important shortcoming. Because matriline members share similar rank and are also genetic relatives, and AFR is known to be heritable at Cayo Santiago (Blomquist 2009a, b), it is unclear to what extent the environment provided by social rank or potential genetic differences among matriline contribute 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 average for the trait (Kruuk 2004; Mrode 1996).

9.2 Explaining Phenotypic Variation in AFR

Quantitative genetic techniques are essentially statistical models that exploit resemblance among relatives and rules of Mendelian inheritance to break down phenotypic variation. In the past, this meant comparisons of a few kinds of relatives in standard statistical designs, such as mother-daughter regression or sibling ANOVAs (Lynch and Walsh 1998; Roff 1997). More recently, evolutionary-minded ecologists and anthropologists have applied the "animal model" to decompose phenotypic variation (Kruuk 2004; Cheverud and Dittus 1992). This method offers two important advantages over its predecessors. First, it easily allows the incorporation of known environmental factors that may affect phenotypes, such as age, birth cohort, or social group membership. Second, it functions well in highly unbalanced cases where animals are not related as standard mother-daughter or sibling pairs, and instead exploits of all the known genealogical relationships among individuals there is phenotypic information on. The animal model is thus more flexible and statistically more powerful.

The animal model is a linear mixed model (9.1) where \mathbf{y} is a vector of phenotypic data (e.g., AFRs), \mathbf{X} a design matrix for fixed effects, \mathbf{b} a vector of fixed effects used for controlling known variation among individuals, \mathbf{Z}_a a design matrix for random effects, \mathbf{a} a vector of random effects such as individual breeding values, and \mathbf{e} the residual error (Kruuk 2004; Lynch and Walsh 1998). Additional random effects, such as maternal effects, can be accommodated by adding another vector and design matrix to the model (e.g., $\mathbf{Z}_m \mathbf{m}$):

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (9.1)$$

I used phenotypic data on 975 females born on Cayo Santiago between the 1965 and 1999 birth cohort, derived from the Cayo Santiago ACCESS demographic database. AFR was treated as an ordinal variable taking only the integer values of

Table 9.1 Descriptive statistics for female age of first reproduction (AFR) and linear model terms. $N=975$

Variable	Minimum	Maximum	\bar{x}	SD
AFR (cohort years)	3	6	4.270	0.586
Age in cohort (days)	100	346	201.607	41.522
Mother's age at birth (years)	3.05	22.86	7.861	3.495
Matriline rank at birth ^a	1	3	1.997	0.805
Birth cohort (calendar year)	1965	1999	1983.807	8.624

^aCoded as high = 1, middle = 2, low = 3

three to six and was calculated as the difference between a female's birth cohort and that of her first offspring regardless of the offspring's sex or survival.

Several other variables were selected or calculated for use as fixed effects in the animal model and exploration of the influence of maternal characteristics on AFR Table 9.1. These were birth cohort, the age of a maturing female within her birth cohort in days after the beginning of the cohort (August 1), and the age of a maturing female's mother when she gave birth to her. Several other variables were explored but dropped from the final analysis because they had very little explanatory value (presence of a maturing female's mother when she was three years old, whether the maturing female was the product of her mother's first reproduction, and the presence of an older sibling born in the birth cohort prior to the one a maturing female was born in to six months of age).

In addition to these variables, annual matriline rank information was shared by John Berard and Donald Sade. I used the matriline rank of a maturing female within her birth group in the year of her birth coded ordinally as high = 1, middle = 2, or low = 3 rank. In most cases, the matriline of a group were divided into thirds and assigned to these categories. In situations where a social group had two matriline, they were scored as high and low. If there were four matriline, the middle-ranking two matriline were both scored as middle. Females in groups with only one matriline were excluded from analysis.

Pedigree information, or the patterns of relatedness, came from maternal records in the demographic database and genetic paternity determination via microsatellites sampled through the end of 2000 (Nurnberg et al. 1998). While the demographic database contained records for nearly 8,000 individuals at the time of this study most were not informative for the quantitative genetic analysis. A reduced pedigree file containing 1,192 individuals was used to indicate relatedness among the 975 females with AFR records analyzed (Fig. 9.1). While 1,162 of them had known mothers, only 221 had known fathers, such that maternities outnumber paternities by about five to one. There are 30 matriline represented in the pedigree file but many are linked by paternities such that there are only 14 separate "families." Nearly all of the individuals (95.6%) are contained within one large pedigree of 1,140 members, while the remaining individuals are in linked in smaller groupings with only three to nine members each. The mean coefficient of relatedness between females with the AFR records used in analysis was 0.0050 ($SD=0.0299$).

Fixed effects were explored in using a general linear model in R (R Development Core Team 2007) prior to running the animal model. Age in cohort, matriline rank at birth, and birth cohort were all highly significant predictors ($P < 0.01$). Mother's age at birth was not significant ($P = 0.218$) but was retained to remove potential variation that might complicate the quantitative genetic estimates. The model R^2 indicates that this set of variables explains about 24% of the variation in AFR, with birth cohort making the largest contribution (SS in Table 9.2). Regression slopes for age in cohort and maternal age were positive indicating later AFR resulted from being born late within a cohort or being born to an older mother (age in cohort $\beta = 0.0030 \pm 0.0005$; maternal age at birth $\beta = 0.0062 \pm 0.0050$). The well-known pattern of higher matriline rank yielding earlier maturation is also illustrated in Fig. 9.2.

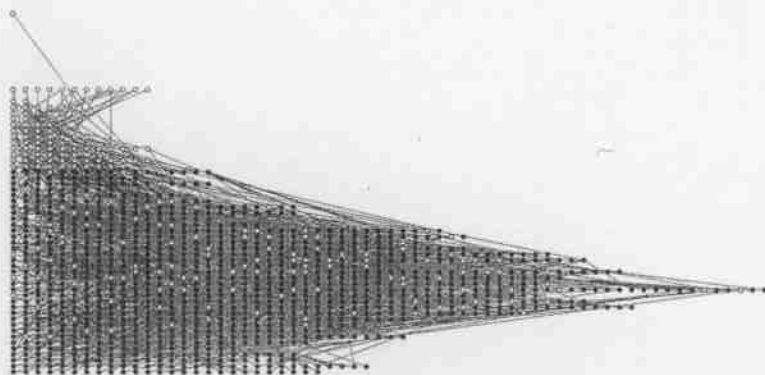


Fig. 9.1 Pedigree(s) of 1,192 Cayo Santiago macaques used in quantitative genetic analysis. Circles indicate females and squares males. Filled symbols identify AFR records used in the analysis. Open symbols are individuals providing pedigree links but phenotypic information was not applicable or not available for them. Each row gives the members of a birth cohort starting with one individual from 1938 at the top, followed in larger numbers after 1951, and finishing at 1999 on the bottom row

Table 9.2 Linear model analysis of variance table predicting female AFR at Cayo Santiago ($R^2=0.242$)

	SS	df	F	P
Age in cohort	9.56	1	35.32	<0.001
Mother's age at birth	0.41	1	1.52	0.218
Matriline rank at birth	3.09	2	5.71	0.003
Birth cohort	69.24	34	7.52	<0.001
Residuals	253.35	936		

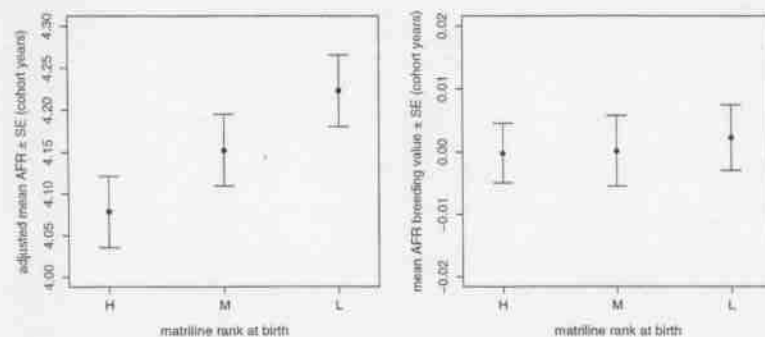


Fig. 9.2 Phenotypic (left) and breeding value (right) mean differences in female AFR among matriline rank levels at Cayo Santiago. Phenotypic values are adjusted means from the linear model evaluated for a maturing female who was born 200 days into the 1965 birth cohort to a 10-year-old mother

Variance components were computed running the animal model in WOMBAT (Meyer 2007). Age in cohort and mother's age at birth were used as linear covariates while matriline rank at birth and birth cohort were entered as multi-level fixed effects. Three random effects in the model were animal identity to account for additive genetic variation, maternal identity to estimate any maternal effects, and unexplained residual error. These sources are assumed to be uncorrelated such that the phenotypic variance is the sum of its variance components ($V^P = V_A + V_M + V_R$).

9.3 Results

The reduction in phenotypic variance by accounting for the fixed effects variables was about 21% of the total (0.343–0.270), consistent with the general linear model R^2 (Tables 9.2 and 9.3). Additive genetic variation accounted for about 15% of the remaining phenotypic variation ($h_{\text{anim}}^2 = 0.159 \pm 0.065$; $t_{975} = 2.293$, $P = 0.011$, $P = 0.011$) or 12% of the total phenotypic variance (h_{total}^2). Wilson (2008) proposed h_{total}^2 is better for comparisons among published heritability estimates because it does not depend on the fixed effects used in the animal model. The maternal effect was estimated to be zero, leaving about 67% of the total phenotypic variance unexplained (Table 9.3). Dropping matriline rank at birth as a fixed effect caused a very minor increase in the heritability estimate but did not change the maternal effect. Unfortunately, the small number of paternities in the pedigrees used does not allow for very good separation of additive genetic and maternal variance in this data set (Fig. 9.1) and this result of $m=0$ could be regarded with some suspicion.

9.4 Genetic vs. Environmental Causes of AFR Differences by Matriline Rank

An additional result of running the animal model just described is the generation of predicted breeding values (PBVs; Kruuk 2004; Mrode 1996). These are estimates of how much the alleles each individual carries caused its AFR to depart from what

Table 9.3 Variance components and ratios for female AFR at Cayo Santiago

Variance component \pm SE	Ratio \pm SE
V_A	0.040 \pm 0.018
V_M	0.000 \pm 0.010
V_R	0.230 \pm 0.019
V_{mat}^*	0.270 \pm 0.013
$V_{\text{total}}^{\dagger}$	0.343
	$h_{\text{anim}}^2 = 0.149 \pm 0.065$
	$m = 0.000 \pm 0.036$
	$r = 0.851 \pm 0.065$
	$h_{\text{total}}^2 = 0.117$
	Fixed effects = 0.211

*Phenotypic variance after fixed effects are removed
 \dagger Total phenotypic variance including fixed effects

would be expected given the fixed effects used in the model (age in cohort, maternal age, matriline rank, and birth cohort) and the known variance components. While rank-related differences in AFR are well documented phenotypically, using PBVs could identify genetic causes for those phenotypic trends.

Postma (2006) argued that exploration of breeding values must be done with a full understanding of the reliability of predicted breeding values and clear statement of null hypotheses when testing for trends within them. When individuals are not randomized among environments, a predicted breeding value 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 predicted breeding values 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 predicted breeding values 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 the predicted breeding values are accurate reflections of the true breeding value.

Once generated, predicted breeding values can be analyzed like phenotypic data using standard statistical software (Kruuk 2004). As just noted, however, 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 predicted breeding values. To demonstrate AFR records in the Cayo Santiago pedigree are well-connected, I calculated the percentage of close relatives (coefficient of relatedness ≥ 0.125) in matriline rank categories different from the rank category of each individual (Garant et al. 2005). Pair-wise coefficients of relatedness were determined by the `makeA()` function in R's pedigree package (Coster 2008).

9.5 Results

The predicted breeding values show no rank-related trends (ANOVA $F_{2,972} = 0.064$, $P > 0.93$; Fig. 9.2). This implies that the additive genetic variation previously noted for AFR is essentially randomly distributed among the different rank levels, and, importantly, that the well-known phenotypic differences are simply the result of the beneficial environment shared by females of higher social rank.

The AFR reliability and connectivity among rank categories both suggest that the lack of trend in the PBVs is trustworthy. The reliability is 0.221 (0.009/0.040) which is 48% greater than the heritability. Furthermore, about 25–30% of a female's close relatives come from different matriline rank categories, suggesting high amounts of connectivity between the rank levels (Table 9.4).

Table 9.4 Connectivity between rank categories where the coefficient of relatedness between individuals was 0.125 or more

	High	Middle	Low	Total pairs	Different (%)
High	1,759	458	214	2,431	27.64
Middle		2,290	358	3,106	26.27
Low			1,498	2,070	27.63

9.6 Discussion

The general picture of female maturation from these results is one of great environmental responsiveness, with a small but significant genetic component. The heritability estimate for AFR for the Cayo Santiago females differs from the one previous estimate for a nonhuman primate population. It is much higher in captive baboons that live in a much more controlled environment at the Southwest Foundation for Biomedical Research ($h^2 = 0.87$, Williams-Blangero and Blangero 1995). Quantitative genetic studies on living and historical human populations indicate that a wide range of heritabilities can be found for menarcheal age and AFR (e.g., 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 for AFR at Cayo Santiago is unsurprising. Additional sources of variation will be contained in the residual variance (V_R) for AFR. These include genetic sources such as dominance and epistasis and other environmental factors beyond the fixed effects used in the animal model. For example, individual rank differences within matriline might also explain some variance.

The larger cohort effects on AFR incorporate a wide variety of potential inter-annual differences between 1965 and 1999. Population and group size or age structure may be among the most important of these (Bercovitch and Berard 1993) while climatic factors or changes in population management may play a role as well (Rawlins and Kessler 1985, 1986; Sade et al. 1985). A small amount of additive genetic variance also might be mistakenly contained within the cohort variance here, which would depress the heritability. This would be caused by the concentration of paternity among few sires within birth cohorts (Widdig et al. 2003). However, because cohorts have multiple sires and sires typically produce offspring in multiple cohorts, it is unlikely that this effect is very large.

Maternal effects on AFR are even less clear and require care to communicate the manner in which there are or are not maternal effects on this life history trait. Several variables that could be interpreted as maternal characteristics (e.g., mother's age, matriline rank at birth, and perhaps even age within cohort) systematically contribute to advance or delay in AFR. However, maternal age and age in cohort are transient phenomena that will not contribute to similarity among a mother's offspring.

The stability of matriline rank should increase similarity among offspring. However, the intergenerational stability of rank also suggests that rank could be interpreted as a direct effect of offspring environment rather than a maternal effect (Cheverud and Wolf 2009). Regardless of the strength of the relationships or interpretation of these variables, the animal model estimate for $m=0$ implies that maternal identity does not contribute to resemblance among maturing females any more than is already expected by Mendelian inheritance. This is consistent with studies of domesticated or lab animals on morphology where maternal effects commonly decline with offspring age such that AFR may be at the terminal age limit of their detectable strength (Wilson and Réale 2006; Atchley 1984). However, the interpretation of this result should also be cautious because of the low number of paternities in the pedigrees that limit the separation of additive and maternal variance. Increasing the number of paternities, especially if adequate tissue samples for individuals born in the 1950s–1970s were available to be genotyped, could resolve this question.

The lack of breeding value differences among rank categories is important for at least two reasons (Blomquist 2009a). First, it verifies the long-assumed position that matriline differences in life history traits are due to the environment provided by rank and not genetic differences among the matrilines (Silk 1984). This is encouraging for field observers 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). Second, it implies some aspects of the evolutionary dynamics of female age of first reproduction at Cayo Santiago and perhaps more generally among female cercopithecines with strong, nepotistic dominance hierarchies. 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, which is provided by the animal model (Kruuk 2004). Nevertheless, selection on age of first reproduction 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 2009c).

Like many studies carried out at Cayo Santiago, this one would likely have been impossible in a field setting. Sufficient pedigree information and life history data are simply not currently available at most primate field sites. Cayo Santiago is exceptional for its temporal depth and topical breadth of information ranging from behavior, demography, and genetics through morphology, immunology, and endocrinology. The potential synergy of the ever-expanding data set on this thoroughly studied population is exciting.

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Chapter 10

Costs of Reproduction Among Rhesus Macaque Females on Cayo Santiago

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10.1 Introduction

Reproduction is energetically costly for mammalian females (gestation and lactation and, consequently, is likely to be associated with reduced survival (Stearns 1989, 1992; Roff 2002), particularly when resources are poor. Higher mortality may be associated with birth-related costs, which may be the consequence of elevated circulating levels of cortisol (see McEwen et al. 1997, for a review). If the hypothalamic (HPA) axis is hyperactivated in post-partum females during periods of either the energetic demands of lactation or the associated stressors, immune function may become impaired, potentially making females more vulnerable to diseases and to increased risk of mortality.

Survival costs of reproduction have been documented for a number of species. Among seasonally breeding Columbian and Richardson's (*Spermophilus columbianus* and *Spermophilus richardsonii*), mortality is highest in the birth season and during the period of lactation (Locklear 1990; Michener 1998; Neuhaus and Pelletier 2001) (*Papio* spp.), mortality rates are highest among lactating and pre-reproductive females (Cheney et al. 2004).

The terminal investment and senescence hypotheses both predict that reproduction should increase with age. According to the sen-

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