biology
letters

Trade-off between age of first reproduction and survival in a female primate

Gregory E. Blomquist

Supplementary data	"Data Supplement" http://rsbl.royalsocietypublishing.org/content/suppl/2009/03/06/rsbl.2009.0009.DC1.html
References	**This article cites 25 articles, 8 of which can be accessed free** http://rsbl.royalsocietypublishing.org/content/5/3/339.full.html#ref-list-1
Subject collections	Articles on similar topics can be found in the following collections ecology (571 articles) evolution (679 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Biol. Lett.* go to: **http://rsbl.royalsocietypublishing.org/subscriptions**

Trade-off between age of first reproduction and survival in a female primate

Gregory E. Blomquist*

Department of Anthropology, University of Missouri, Columbia, MO 65211, USA
*blomquistg@missouri.edu

Trade-offs are central to life-history theory but difficult to document. Patterns of phenotypic and genetic correlations in rhesus macaques, *Macaca mulatta*—a long-lived, slow-reproducing primate—are used to test for a trade-off between female age of first reproduction and adult survival. A strong positive genetic correlation indicates that female macaques suffer reduced adult survival when they mature relatively early and implies primate senescence can be explained, in part, by antagonistic pleiotropy. Contrasts with a similar human study implicate the extension of parental effects to later ages as a potential mechanism for circumventing female life-history trade-offs in human evolution.

1. INTRODUCTION

Trade-offs among traits that contribute to lifetime fitness are ubiquitous features of models of life-history evolution (Stearns 1989). Trade-offs occur when organisms pay a fitness cost, such as delaying sexual maturation, to gain a fitness benefit, such as increased chances of survival later in life. A genetic correlation results when alleles at a locus influence both traits involved in a trade-off (Roff 2002). Despite the importance of trade-offs to life-history theory, they have been notoriously difficult to document (Roff & Fairbairn 2007). One reason for this problem is that although trade-offs should result from the partitioning of finite resources, environmental variation in resource acquisition can mask the genetic patterns expected from trade-offs (van Noordwijk & de Jong 1986). Phenotypic correlations between life-history traits are thus less likely to reflect trade-offs than their genetic correlations (Reznick 1985).

The characteristic ability of humans to control the resources available within social groups (Kaplan & Robson 2002; Lee 2008) complicates the empirical exploration of trade-offs in human populations. Also, quantitative genetic approaches have rarely been applied to human life-history variation and only in recent agricultural or industrialized settings (e.g. Westendorp & Kirkwood 1998; Kirk *et al.* 2001; Pettay *et al.* 2005). Furthermore, the kinds of

trade-offs often explored and the non-human taxa in which they have been studied may have little to do with the important trade-offs that have affected females during human evolution (Hawkes & Paine 2006). For these reasons, I applied quantitative genetic techniques to explore female life-history trade-offs in a population of rhesus macaques (*Macaca mulatta*).

The clearest set of trade-offs for female primates are between current reproduction and survival or, more generally, current and future reproduction. The primate emphasis on extended juvenility, long lifespan and reduced reproductive rate implies that much of their ability to attain high fitness depends on their continued survival from year to year (Martin 1990; Kappeler & Pereira 2003). More than 90 per cent of variation in lifetime number of offspring in female rhesus macaques is explained by adult lifespan (figure 1). Simple demographic models of primate life histories also demonstrate that lifetime fitness (λ, finite rate of increase) is most responsive to changes in adult survival rates (Heppell *et al.* 2000).

Trade-offs between current reproduction and survival or future reproduction may act over a variety of time scales. If costs of reproduction have long-term additive or multiplicative consequences, it is comparisons of distant life-history events that will reveal trade-offs (Rose & Charlesworth 1994). Indeed, Williams's (1957) antagonistic pleiotropy theory of ageing hypothesizes the existence of trade-offs mediated by loci having opposing fitness effects on these early and late life-history variables. Genetic correlations between the variables can be used to index these pleiotropic effects and assess the strength of proposed trade-offs. This model has received broad support in experimental investigations and some naturalistic studies (Charlesworth 1994; Hughes *et al.* 2002).

I focus on the relationship between adult survival and female age of first reproduction (AFR)—a key early life-history variable for female primates (Bercovitch & Berard 1993; Charnov & Berrigan 1993; Altmann & Alberts 2005). Furthermore, female AFR is known to be heritable in the study population, making genetic covariance with other life-history traits plausible (Blomquist 2009). A life-history trade-off will be indicated by a *positive* relationship between AFR and adult survival, because when all other factors are held constant, decreasing AFR will increase lifetime fitness (Roff 2002).

2. MATERIAL AND METHODS

I used individual life-history data from a large population of free-ranging rhesus macaques 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 forage on natural vegetation and live in naturally formed social groups (Rawlins & Kessler 1986).

Age of first reproduction (AFR) and survival rates from AFR to four different ages were measured (11, 16, 21 and 26 years). Data were selected to ensure precision of age estimates, omit potentially pathological individuals and avoid biasing survival rates to older ages by including recent birth cohorts in which only young individuals could have died (see the electronic supplementary material for details of data selection and analysis). Pearson's correlations among the life-history variables were calculated in R (R Development Core Team 2007).

Quantitative genetic analyses used univariate and bivariate 'animal models' (Kruuk 2004), relying on a large pedigree of the study population, which included paternities determined by
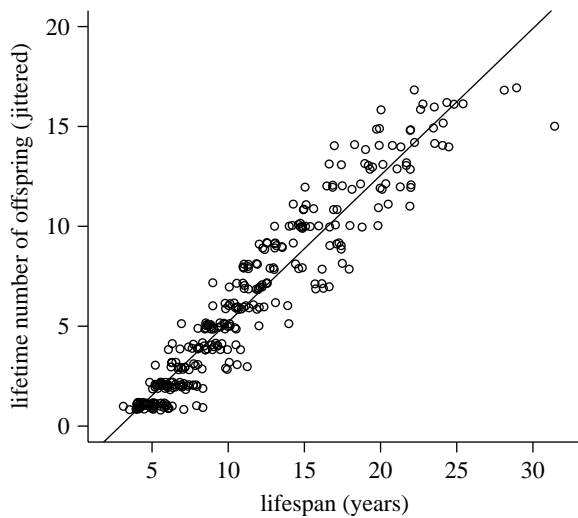
Figure 1. Regression of lifetime number of offspring on lifespan for female rhesus macaques at Cayo Santiago ($p < 0.0001$, $R^2 = 0.91$). Small random deviations (jittering) are added to number of offspring to expose overlapping points.

microsatellite variation (Nurnberg *et al.* 1998). Additive genetic and residual (co)variance components and their standard errors were estimated in VCE 5.1 (Groeneveld & Kovac 1990). These are reported as genetic or residual correlations and heritabilities. The significance of a correlation or heritability from zero was tested by comparing the ratio of the value and its standard error to a *t*-distribution with degrees of freedom equal to the number of observations (Kruuk *et al.* 2000). Where multiple heritability estimates were available, their mean is reported in table 1.

3. RESULTS

Phenotypic correlations between AFR and each survival rate are all positive but very weak (range: 0.083–0.132). The largest of these correlations are for the younger survival rates (11 and 16 years) and both are statistically significant or nearly so (table 1). The implications of these small positive correlations are that any trade-off between early reproduction and survival is very weak and may only affect survival over the first decade after maturation.

Quantitative genetic analysis indicates modest heritabilities of AFR and survival rates (0.128–0.386). All of these are significantly greater than zero except the smallest, for survival to age 11 (table 2). Genetic correlations are all large and positive (0.476–0.706), indicating a strong trade-off between age of first reproduction and later life survival (table 1). None of the residual correlations between AFR and survival rates are significant, although most of them are weakly negative, implying that environmental effects that promote early maturation will raise later life survival. It is this combination of strong positive genetic correlations and weak negative residual correlations that results in the weak positive phenotypic values.

4. DISCUSSION

The strong positive genetic correlation between female AFR and adult survival identifies an important genetically mediated constraint on the reproductive decision making of female primates. Heavy investment in offspring production early in life imposes a cost of reduced lifespan for female macaques.

Table 1. Phenotypic (r_P), genetic (r_A) and residual (r_R) correlations between female age of first reproduction (AFR) and adult survival rates to age x (s_x). Standard errors are given in parentheses and p-values in italics below the correlation (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).

	s_{11}	s_{16}	s_{21}	s_{26}
r_P	0.1094*	0.1323**	0.1008	0.0834
	0.065	*0.032*	*0.141*	*0.288*
r_A	0.5900*	0.5945***	0.4763***	0.7062**
	(0.320)	(0.215)	(0.170)	(0.283)
	0.067	*0.006*	*0.006*	*0.013*
r_R	0.0229	−0.0281	−0.0234	−0.0231
	(0.063)	(0.068)	(0.082)	(0.076)
	0.716	*0.680*	*0.775*	*0.761*

Using the estimated genetic variances and covariances of AFR and survival rate to age 16, the cost of maturing 1 year earlier is a loss of approximately 11 months of adult life (see the electronic supplementary material). The weaker phenotypic pattern may result from variation in resource abundance or psychosocial stress, which causes earlier maturation and higher survival or later maturation coupled with reduced survival (van Noordwijk & de Jong 1986; Roff & Fairbairn 2007).

While there are a number of phenotypic studies that have suggested associations between early reproduction and longevity in humans (Le Bourg 2007), the only previous estimate of a genetic correlation between AFR and indicators of lifespan or survival for any primate is from pre-industrial Finns (Pettay *et al.* 2005). The correlation reported was also strongly positive, but it should be regarded with caution because AFR had a non-significant heritability. The macaque results are consistent with this single human estimate. However, AFR in Finns was strongly influenced by maternal effects, while these are very small for female macaques (Blomquist 2009). An intriguing interpretation of this difference is that humans have evolved mechanisms to circumvent life-history trade-offs that are expressed in other female primates, possibly through the deliberate control and redistribution of resources within social groups, perhaps along kin lines, that results in the extension of parental effects to later ages (Cheverud & Moore 1994; Hawkes *et al.* 1998; Kaplan & Robson 2002; Lee 2008). Similar investigations of human groups under different subsistence modes and residence system may resolve this question (Marlowe 2005; Quinlan 2008).

Table 2. Descriptive statistics, coefficients of additive genetic variation (CV_A) and heritabilities (h^2) of female life-history traits. The p-values are for tests of the null hypothesis $h^2 = 0$.

	n	range	mean	s.d.	CV_A	$h^2 \pm$ s.e.	p-value
AFR	1067	3–6	4.27	0.5728	0.91	0.1285 ± 0.034	< 0.001
s_{11}	286	0.28–1	0.82	0.2192	0.74	0.1279 ± 0.094	0.177
s_{16}	264	0.19–1	0.69	0.2630	2.58	0.2627 ± 0.092	0.005
s_{21}	214	0.15–1	0.58	0.2683	4.67	0.3861 ± 0.121	0.002
s_{26}	164	0.12–1	0.45	0.2369	3.86	0.3206 ± 0.106	0.003

Altmann, J. & Alberts, S. C. 2005 Growth rates in a wild primate population: ecological influences and maternal effects. *Behav. Ecol. Sociobiol.* **57**, 490–501. (doi:10. 1007/s00265-004-0870-x)

Bercovitch, F. B. & Berard, J. D. 1993 Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behav. Ecol. Sociobiol.* **32**, 103–109. (doi:10.1007/BF00164042)

Blomquist, G. E. 2009 Fitness-related patterns of genetic variation in rhesus macaques. *Genetica* **135**, 209–219. (doi:10.1007/s10709-008-9270-x)

Charlesworth, B. 1994 *Evolution in age-structured populations*, 2nd ed. New York, NY: Cambridge University Press.

Charnov, E. L. & Berrigan, D. 1993 Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evol. Anthropol.* **1**, 191–194. (doi:10.1002/evan.1360010604)

Cheverud, J. M. & Moore, A. J. 1994 Quantitative genetics and the role of the environment provided by relatives in behavioral evolution. In *Quantitative genetic studies of behavioral evolution* (ed. C. R. B. Boake), pp. 67–100. Chicago, IL: University of Chicago Press.

Groeneveld, E. & Kovac, M. 1990 A generalized computing procedure for setting up and solving mixed linear models. *J. Dairy Sci.* **73**, 513–531.

Hawkes, K. & Paine, R. R. (eds) 2006 *The evolution of human life history*. Santa Fe, NM: School of American Research Press.

Hawkes, K., O'Connell, J. F., Jones, N. G., Alvarez, H. & Charnov, E. L. 1998 Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl Acad. Sci. USA* **95**, 1336–1339. (doi:10.1073/pnas.95.3. 1336)

Heppell, S. S., Caswell, H. & Crowder, L. B. 2000 Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* **81**, 654–665. (doi:10.1890/0012-9658(2000)081[0654:LHA EPP] 2.0.CO;2)

Hughes, K. A., Alipaz, J. A., Drnevich, J. M. & Reynolds, R. M. 2002 A test of evolutionary theories of aging. *Proc. Natl Acad. Sci. USA* **99**, 14286–14291. (doi:10. 1073/pnas.222326199)

Kaplan, H. S. & Robson, A. J. 2002 The emergence of humans: the coevolution of intelligence and longevity with intergenerational transfers. *Proc. Natl Acad. Sci. USA* **99**, 10221–10226. (doi:10.1073/pnas.152502899)

Kappeler, P. M. & Pereira, M. E. 2003 *Primate life histories and socioecology*. Chicago, IL: University of Chicago Press.

Kirk, K. M., Blomberg, S. P., Duffy, D. L., Heath, A. C., Owens, I. P. & Martin, N. G. 2001 Natural selection and quantitative genetics of life-history traits in western women: a twin study. *Evolution* **55**, 423–435. (doi:10. 1111/j.0014-3820.2001.tb01304.x)

Kruuk, L. E. B. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. B.* **359**, 873–890. (doi:10.1098/rstb.2003.1437)

Kruuk, L. E. B., Clutton-Brock, T. H., Slate, J., Pemberton, J. M., Brotherstone, S. & Guinness, F. E. 2000 Heritability of fitness in a wild mammal population. *Proc. Natl Acad. Sci. USA* **97**, 698–703. (doi:10. 1073/pnas.97.2.698)

Le Bourg, E. 2007 Does reproduction decrease longevity in human beings? *Ageing Res. Rev.* **6**, 141–149. (doi:10. 1016/j.arr.2007.04.002)

Lee, R. 2008 Sociality, selection, and survival: simulated evolution of mortality with intergenerational transfers and food sharing. *Proc. Natl Acad. Sci. USA* **105**, 7124–7128. (doi:10.1073/pnas.0710234105)

Marlowe, F. W. 2005 Hunter–gatherers and human evolution. *Evol. Anthropol.* **14**, 54–67. (doi:10.1002/evan. 20046)

Martin, R. D. 1990 *Primate origins and evolution: a phylogenetic reconstruction*. Princeton, NJ: Princeton University Press.

Nurnberg, P. *et al.* 1998 Paternity assessment in rhesus macaques (*Macaca mulatta*): multilocus DNA fingerprinting and PCR marker typing. *Am. J. Primatol.* **44**, 1–18. (doi:10.1002/(SICI)1098-2345(1998)44:1< 1::AID-AJP1>3.0.CO;2-#)

Pettay, J. I., Kruuk, L. E. B., Jokela, J. & Lummaa, V. 2005 Heritability and genetic constraints of life-history trait evolution in preindustrial humans. *Proc. Natl Acad. Sci. USA* **102**, 2838–2843. (doi:10.1073/pnas.040 6709102)

Quinlan, R. J. 2008 Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. *Evol. Anthropol.* **17**, 227–238. (doi:10.1002/evan. 20191)

R Development Core Team 2007 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rawlins, R. G. & Kessler, M. J. (eds) 1986 *The cayo santiago macaques: history, behavior, and biology*. Albany, NY: SUNY Press.

Reznick, D. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267. (doi:10. 2307/3544698)

Roff, D. A. 2002 *Life history evolution*. Sunderland, MA: Sinauer Associates.

Roff, D. A. & Fairbairn, D. J. 2007 The evolution of trade-offs: where are we? *J. Evol. Biol.* **20**, 433–447. (doi:10.1111/j.1420-9101.2006.01255.x)

Rose, M. R. & Charlesworth, B. 1981 Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. *Genetics* **97**, 173–186.

Stearns, S. C. 1989 Trade-offs in life history evolution. *Funct. Ecol.* **3**, 259–268. (doi:10.2307/2389364)

van Noordwijk, A. J. & de Jong, G. 1986 Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–142. (doi:10.1086/284547)

Westendorp, R. G. & Kirkwood, T. B. 1998 Human longevity at the cost of reproductive success. *Nature* **396**, 743–746. (doi:10.1038/25519)

Williams, G. C. 1957 Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411. (doi:10.2307/2406060)