



Selection on adult female body size in rhesus macaques

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ABSTRACT

Body size is a critical descriptor of animal biology with many ecological, behavioral, and physiological correlates. Size differences among species or between populations are often explained by adaptive scenarios invoking the action of selection, although studies of selection in action on primate body size, or other phenotypic traits, are very rare. We document directional selection for larger skull and postcranial size in the skeletons of female semi-free ranging rhesus macaques (*Macaca mulatta*) from Cayo Santiago, born between 1957 and 1982. Larger females live to later ages and consequently give birth to more offspring. Despite selection for larger size, there are indications of a trend toward generally smaller size in the same birth cohorts. This trend is provisionally attributed to increasing population density, though other environmental factors may play a role. Small selection differentials and low heritabilities also limit the genetic response to selection. Alternative explanations for increasing adult size in the skull and postcranium, such as continued adult growth or pathological bone deposition, do not adequately explain the observed age-related trends and are inconsistent with longitudinal studies of adult skeletal change.

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Introduction

Body size is an important descriptor of organisms, having many morphological, physiological, life history, and ecological correlates (Gould, 1977; Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984; Jungers, 1985; Harvey, 1990; Charnov, 1993; Brown and West, 2000; Ruff, 2002; van Bergen and Phillips, 2005). Interspecific and intraspecific size differences and scaling relationships are explained through the past action of natural or sexual selection. However, the macro- and microevolutionary scale of body size adaptation can be remarkably different (Kozlowski and Weiner, 1997; Gordon, 2006a,b). Currently, studies of within-population variation documenting phenotypic selection in action on wild or free ranging groups are exceedingly rare for primates (e.g., DeGusta et al., 2003; Lawler et al., 2005), though other vertebrate taxa have been more thoroughly investigated (Endler, 1986; Kingsolver et al., 2001).

Most morphological traits, including body size, are thought to be maintained near optimum by selection against extreme values (i.e., stabilizing selection) where the fitness benefit/cost ratio of a particular size is maximized (Preziosi and Fairbairn, 2000). However, many cases of directional selection in the wild are known and have been related to changing environmental conditions that

likely alter the costs or benefits of being a particular size (Garant et al., 2004; Pelletier et al., 2007; Ozgul et al., 2009). An alternative is that selection is primarily directional on morphological traits, but direction of favored change fluctuates frequently with environmental changes (Grant and Grant, 2002).

Measuring patterns of selection on primate body size can help clarify debates on the socioecology and evolution of sexual dimorphism or body size in general. The majority of hypotheses about primate and hominin dimorphism have been generated by interspecific comparisons, which, while valuable, cannot measure the mechanisms suggested to lead to sexual dimorphism (Blanckenhorn, 2005). Similarly, female hominin energetics, and presumably fitness, have been intimately linked to body size (Aiello and Key, 2002; Aiello and Wells, 2002), such that the energetic demands of female body size increase in *Homo* are thought to have been offset by cooperative care of infants or sexual division of labor. While intriguing, we currently lack any demonstration that female body size variation within primate populations has any effect on fitness.

Explanations for dimorphism typically invoke sexual selection. Strong dimorphism is generally expected when mate competition in a highly polygynous mating system favors body size increase in males, although other factors are likely involved (Plavcan, 2001; Lindenfors, 2002; Clutton-Brock, 2004). Importantly, body size increase in females has been modeled as a correlated response due to selection only on males and a genetic correlation between the sexes (Lande, 1980; Smith and Cheverud, 2002; Gordon, 2006a). However, there are many potential advantages to large

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female body size including increased fecundity by reducing inter-litter intervals or increased frequency of multiple births, avoidance of obstetrical complications, increased offspring mass and offspring survival rates, a more male-biased sex ratio of offspring, ability to attract higher quality mates, and greater locomotor or foraging efficiency (Ralls, 1976; Isaac, 2005). Indeed, in the review by Kingsolver et al. (2001), all but one study of selection in action on female size in vertebrate populations demonstrated positive selection differentials or gradients (slope of the fitness measure on size regression or multiple regression; Lande and Arnold, 1983). Gordon (2006b) also suggests that frequent negative scaling of male/female dimorphism and female size among congeneric primate species is primarily the result of stronger natural selection on female size among species that share similar mating systems.

Macaques are a valuable taxon for the study of body size evolution and dimorphism because the genus contains a large number of species that have a wide range of body sizes and body dimorphism measures (Smith and Jungers, 1997). Although all macaques live in multi-male multi-female groups, there are also notable differences in dominance style and male mating tactics (Thierry, 2007). Rhesus macaques are among the least dimorphic but most nepotistic and despotic macaques (Smith and Cheverud, 2002; Thierry et al., 2004).

Demonstration of phenotypic selection in action on primate populations is uncommon, likely due to the need for long-term demographic data to measure reproductive fitness and phenotypic measurements on large numbers of individuals. We were only able to identify four primate populations with studies of phenotypic selection. DeGusta et al. (2003) showed M^1 size was under positive directional selection in the Barro Colorado *Alouatta palliata*. Leigh et al. (2008) found differences in male fertility related to canine size in semi-free ranging *Mandrillus sphinx*. Lawler et al. (Lawler et al., 2005; Lawler, 2006, 2008) measured selection acting on limb and body proportions in wild *Propithecus verreauxi*.

We took a similar approach to DeGusta et al. (2003), who used skeletons of deceased monkeys and estimates of age at death to document phenotypic selection (cf. Jones et al., 2000). Our study population, the Cayo Santiago macaques, has several advantages in allowing for precisely known ages at death, measures of reproductive output, and a large number of matching complete skeletons for collection of phenotypic data. The availability of phenotypic data from animals born over several decades also allows the assessment of temporal trends that could reflect microevolutionary response to phenotypic selection (Grant and Grant, 1995; Reale et al., 2003a; Garant et al., 2004) or changing environmental circumstances of the population (Kruuk et al., 2003; Sinclair and Parkes, 2008).

Materials

Population attributes and data selection

Cayo Santiago is a 15.2 ha Caribbean island located 1 km off the southeast coast of Puerto Rico. Rhesus macaques ($N = 409$) were introduced in 1938 from diverse sources in India, and have been monitored nearly continuously since 1956 (Sade et al., 1985; Rawlins and Kessler, 1986). The animals are fed commercial monkey chow daily and are provided water *ad libitum*. The population has recently been managed through the annual cull of randomly selected one- and two-year olds and previously through periodic removal of social groups. The total size of the population was approximately 175 individuals in the mid-1950s but is currently maintained near 1000 individuals, all of known age and genealogies. Monkeys live in naturally formed social groups, matings are unmanaged, and no

veterinary interventions are performed. Rhesus macaques on Cayo Santiago have a Winter-Spring birth season that results in the population being divisible into well-defined birth cohorts (Rawlins and Kessler, 1985).

Skeletal materials from 66 mature females born between 1957 and 1982 that had reproduced at least once (per the Cayo Santiago ACCESS demographic database), and died of natural causes at ages greater than 6.5 years were measured. The minimum age criterion was used to eliminate females that might still be growing. All long bone epiphyses are fused by this age in the Cayo Santiago sample (Cheverud, 1981). The birth cohort limits were set to ensure females from all the recent cohorts had the potential to live to advanced ages and be present in the skeletal collection. All specimens had been prepared by simple water maceration, which should not impact skeletal dimensions.

Seven postcranial dimensions were recorded with digital sliding calipers to the nearest hundredth millimeter. All skeletons were double measured on separate days by GEB. When left and right elements were present, both were double measured and their mean used in the analysis. A geometric mean of the seven postcranial measurements (humerus length, radius length, third metacarpal length, femur length, tibia length, third metatarsal length, and clavicle length) was used as an index of postcranial size (Jungers et al., 1995). Measurement error was low; the mean inter-trial difference in the postcranial geometric means was 0.022% (maximum: 0.591%).

Cranial size was taken to be the centroid size (Zelditch et al., 2004) of four basicranial and neurocranial landmarks: basion, bregma, and the lateral margin of the left and right glenoid tubercles. The landmark coordinates were aligned by Procrustes superimposition, implemented in the shapes package for R (Dryden, 2008). These regions were selected because they have been reported to show the least age-related change in a Cayo Santiago female skeletal sample (Wang et al., 2007) and should not reflect potential adult skeletal changes. Measurement error was low; the mean inter-trial difference in the cranial centroid sizes was 0.813% (maximum: 2.187%) (Table 1).

We used two variables as proxies for individual fitness when assessing selection on skeletal size. Age at death and number of offspring born, regardless of infant sex and survival, were both derived from the Cayo Santiago ACCESS demographic database. Both of these variables have roughly normal distributions that make them amenable as dependent variables in ordinary least-squares regression. In addition, we recorded population density during the period a female was growing as the January first population size of the colony for 1959–1987, to calculate a 6-year average population size from each female's birth year through fifth year of life (range of annual population sizes: 224–1134). We limited our analysis of selection to a set of females with both postcranial and cranial size measurements. In addition, one female was excluded because of an experimental treatment affecting her fertility and one because of extreme outlier status (final $N = 55$). Slightly larger numbers were available for exploring temporal and density-related trends in size (range: 59–62).

Table 1
Descriptive statistics of the Cayo Santiago female sample.

	N	Mean	SD	min	max
Age at death	66	12.83	5.217	6.563	31.42
Number of offspring born	66	7.20	3.76	1	15
Cranial centroid size	61	66.12	2.276	58.92	70.74
Postcranial geometric mean	62	90.59	3.025	82.90	97.47
Birth cohort	66	1970	6.9370	1957	1982
Mean population size 0–5 years	64	540.30	167.39	314.5	877.2

Body size selection and temporal or density-related trends

Standardized selection differentials (S') are reported as the slope from the least-squares regression of mean-standardized fitness proxies on the z-scored skeletal measurements (Lande and Arnold, 1983; Arnold and Wade, 1984). Slopes of these regressions identify the mean-standardized unit change (i.e., relative fitness) in the fitness proxy expected from a single standard deviation increase in the skeletal measure. Positive selection differentials are evidence of selection for larger size. Stabilizing or disruptive selection was explored by adding a quadratic term to these bivariate regressions, but they are not reported separately because none were significant and had little effect on the linear slope.

In addition, multiple regression is used to assess the independent action of selection on cranial and postcranial size while the other is held constant (standardized selection gradients, β'). Positive selection gradients indicate selection for larger size while the other skeletal variable is unchanged. Gradients isolate the effect of direct selection on a skeletal measure, whereas selection differentials combine these direct effects with indirect selection on the other skeletal trait mediated by their phenotypic correlation (Pearson's $r = 0.502$). Quadratic or correlational terms were explored in the multiple regression models but are not reported because none were significant and all had little effect on the linear slope (Lande and Arnold, 1983; Arnold and Wade, 1984; Phillips and Arnold, 1989).

Temporal and density-related trends in skeletal size are identified from the slope of the bivariate regression of skeletal measures on birth cohort or the mean population size over the first six years of a female's life. Because of the clustering of population sizes, we also used t-tests for mean skeletal size differences between high (>700) and low density (≤ 700) periods. In addition, we used ANCOVA to explore density-related variation in selection on skeletal size by including the high–low density category entered in a linear model along with the size predictor of fitness. Significant size–density interactions would indicate differing selection at high and low density periods, while a significant main effect of density implies a difference in average fitness between high and low density periods.

Results

Body size selection

All selection differentials indicate significant selection for larger body size in female macaques regardless of the skeletal size or fitness indicator used (Table 2, Fig. 1). Selection is stronger for cranial size with both fitness proxies, and differentials are higher for both size indicators in regression with number of offspring.

Multiple regression models provide a similar impression of body size selection in female macaques (Table 3). Standardized selection gradients are positive for both variables, but the gradients for cranial size are 1.8 or 4.4 times larger than postcranial size. Furthermore, the gradients for postcranial size are much smaller than the corresponding differentials and do not differ significantly from zero. This implies that much of the selection on postcranial size identified by the differentials reflects indirect selection on cranial size. Differentials and gradients for cranial size are more consistent, which suggests these differentials primarily reflect direct selection.

Temporal and density-related trends

In contrast to the positive selection differentials and gradients, the average cranial and postcranial size of females in the sample

Table 2

Bivariate regression and ANCOVA models of mean-standardized number of offspring or age at death on z-scored skeletal size measurements. Slopes for the size measures are the standardized selection differentials (S'). Density is coded as 0 = low, 1 = high. $N = 55$ in all models. Significant ($P < 0.05$) size, density, and interaction terms are indicated in bold.

	Intercept	Size	Density	Size \times density	R^2	Model P
Cranial centroid size						
Number of offspring	1.000	0.261			0.268	<0.001
	1.056	0.207	−0.309		0.314	<0.001
	1.059	0.194	−0.245	0.085	0.317	<0.001
Age at death						
	1.000	0.151			0.214	<0.001
	1.003	0.148	−0.018		0.215	0.002
	1.003	0.149	−0.024	−0.008	0.215	0.006
Postcranial geometric mean						
Number of offspring	1.000	0.170			0.114	0.012
	1.085	0.126	− 0.466		0.236	0.001
	1.085	0.126	− 0.466	−0.001	0.236	0.003
Age at death						
	1.000	0.125			0.147	0.004
	1.021	0.114	−0.115		0.165	0.009
	1.020	0.121	0.124	0.024	0.166	0.025

declined significantly over the study period (Table 4, Fig. 2). The size decline in the face of positive directional selection may be due to increased population density. Cranial size declined significantly with increasing density ($P = 0.001$), while there was a weaker nonsignificant trend in postcranial size ($P = 0.080$). T -tests categorizing females as having grown up in high or low density periods gave similar results (cranial: $P = 0.004$, postcranial: $P = 0.176$).

Including density through ANCOVA models had minor effects on the selection analysis (Table 2). There were no significant differences in slope between the high and low density periods in any of the models (density–size interactions, $P > 0.634$). Dropping the interaction, the only significant main effect of density was in the model for number of offspring on postcranial size (density $\beta = -0.466$, $P = 0.006$), although all density effects were negative—females who grew up during high-density periods tended to have lower numbers of offspring or shorter lifespan (Fig. 1). Selection differentials for number of offspring on postcranial size were not significantly different from zero when density was included ($P = 0.05$ in common slope model). Common slope estimates for the skeletal size variables in these models adjusting for mean fitness differences between density levels were very similar to their unadjusted counterparts. There were similar small reductions in selection gradients, particularly on cranial size, when adjusting for density.

Discussion

In females born over two and a half decades on Cayo Santiago, we documented directional selection for larger cranial and postcranial size with a simultaneous decline in the same skeletal measurements. This paradox could be due to a number of intervening factors in predicting temporal change (microevolutionary response) from inferred phenotypic selection. First, the heritabilities for the skeletal measurements are modest (mean h^2 0.407 for seven cranial distances, 0.584 for eight postcranial distances; Blomquist, 2009) and strength of selection on them is relatively weak (Kingsolver et al., 2001). Genetic response in this situation would be small.

Second, response to selection is determined by the additive genetic covariance between a trait and fitness, not their phenotypic relationship that is estimated by selection gradients or differentials (Robertson, 1966; Price, 1970; van Tienderen and de Jong, 1994). Quantitative genetic studies show that the Cayo Santiago female

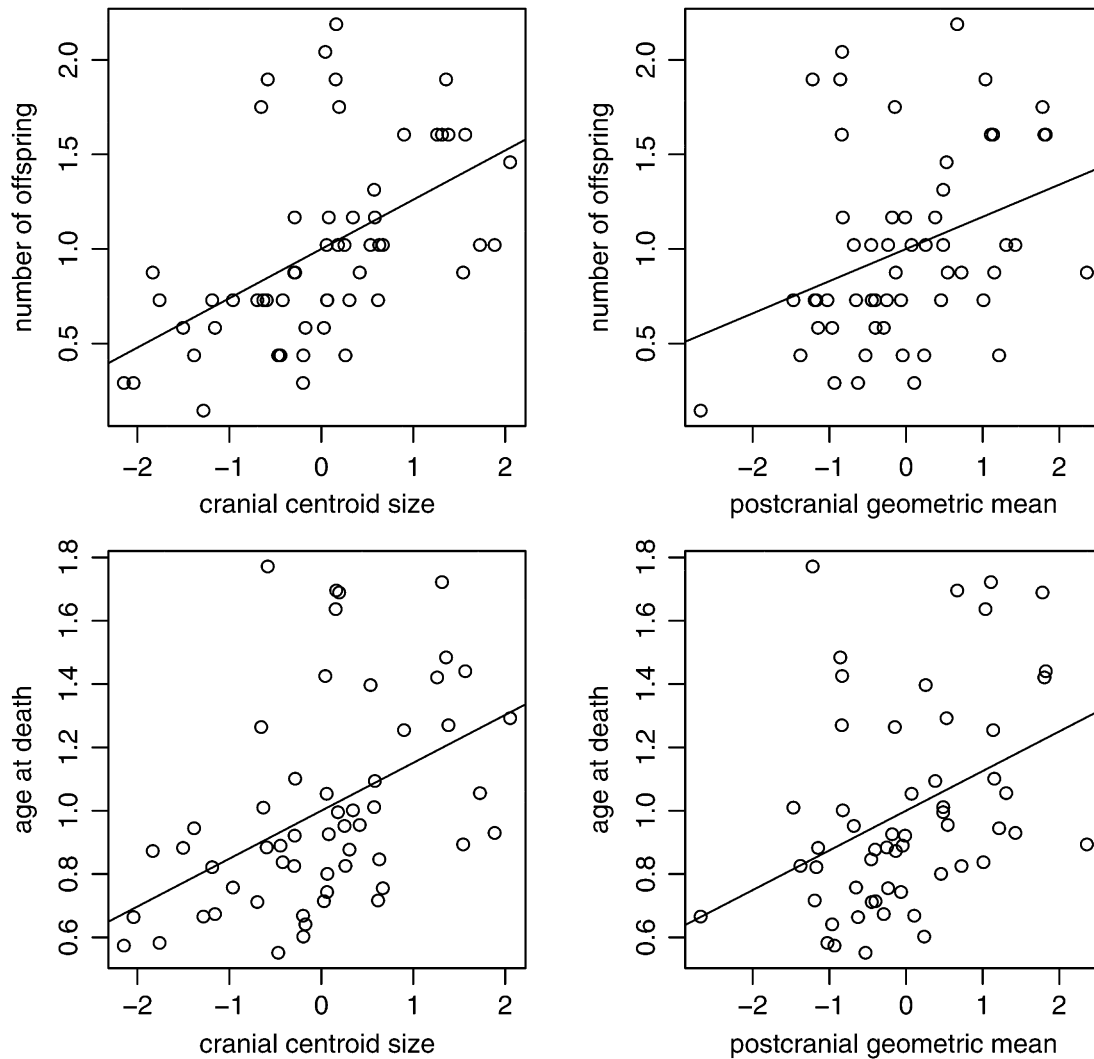


Figure 1. Selection differentials in scatterplots of z-scored cranial centroid size or postcranial geometric mean predicting mean-standardized number of offspring or age at death. Filled circles are females from high-density periods. Solid lines indicate significant regressions through all points (Table 2).

morphological traits cannot meaningfully covary genetically with number of offspring because there is very little additive genetic variance in this measure of fitness among adult females ($h^2 < 0.001 \pm 0.463$ for these 55 females, $h^2 < 0.10$ in larger sets; cf. Blomquist, 2009, 2010). This implies that the positive selection differentials and gradients are the result of selection acting on the environmental component of phenotypic variation such that large size is advantageous, but large females that live to late ages and produce many offspring cannot transmit this quality to their offspring (van Tienderen and de Jong, 1994; Larsson et al., 1998; Kruuk et al., 2002, 2003; Hadfield, 2008). No response can be

Table 3

Multiple regression results predicting mean-standardized number of offspring or age at death for sets of z-scored cranial and postcranial size measurements. Slopes for the size measures are standardized selection gradients (β'). Density is coded as 0 = low, 1 = high. Significant ($P < 0.05$) size and density terms are indicated in bold. $N = 55$ in all models.

	Intercept	Cranium	Postcranium	Density	R^2	Model P
Number of offspring	1.000	0.234	0.053		0.276	<0.001
	1.056	0.183	0.049	-0.305	0.321	<0.001
Age at death	1.000	0.118	0.066		0.245	0.001
	1.003	0.116	0.066	-0.014	0.245	0.002

expected in this situation. A similar point could be made about the difficulty of predicting multivariate response to selection relying only on phenotypic correlations among the morphological measurements. Phenotypic correlations will influence patterns of direct or indirect selection, but it is the additive genetic correlations between these traits that influence inter-generational response (Steppan et al., 2002; Hlusko et al., 2006).

Third, accurately predicting microevolutionary response assumes that the environment remains constant, which is clearly not the case at Cayo Santiago. Density increased dramatically during the study period. Body size declines with increasing density are well known in many mammals (Yom-Tov et al., 2007; Simard et al., 2008; Walker and Hamilton, 2008). Several studies of wild

Table 4

Regression slopes of skeletal measures on birth cohort and average population size for ages 0–5 (density).

	Cranial centroid size				Postcranial geometric mean			
	N	Slope	SE	P	N	Slope	SE	P
Birth cohort	61	-0.123	0.039	0.002	62	-0.116	0.056	0.044
Density	59	-0.006	0.002	0.001	60	-0.004	0.002	0.080

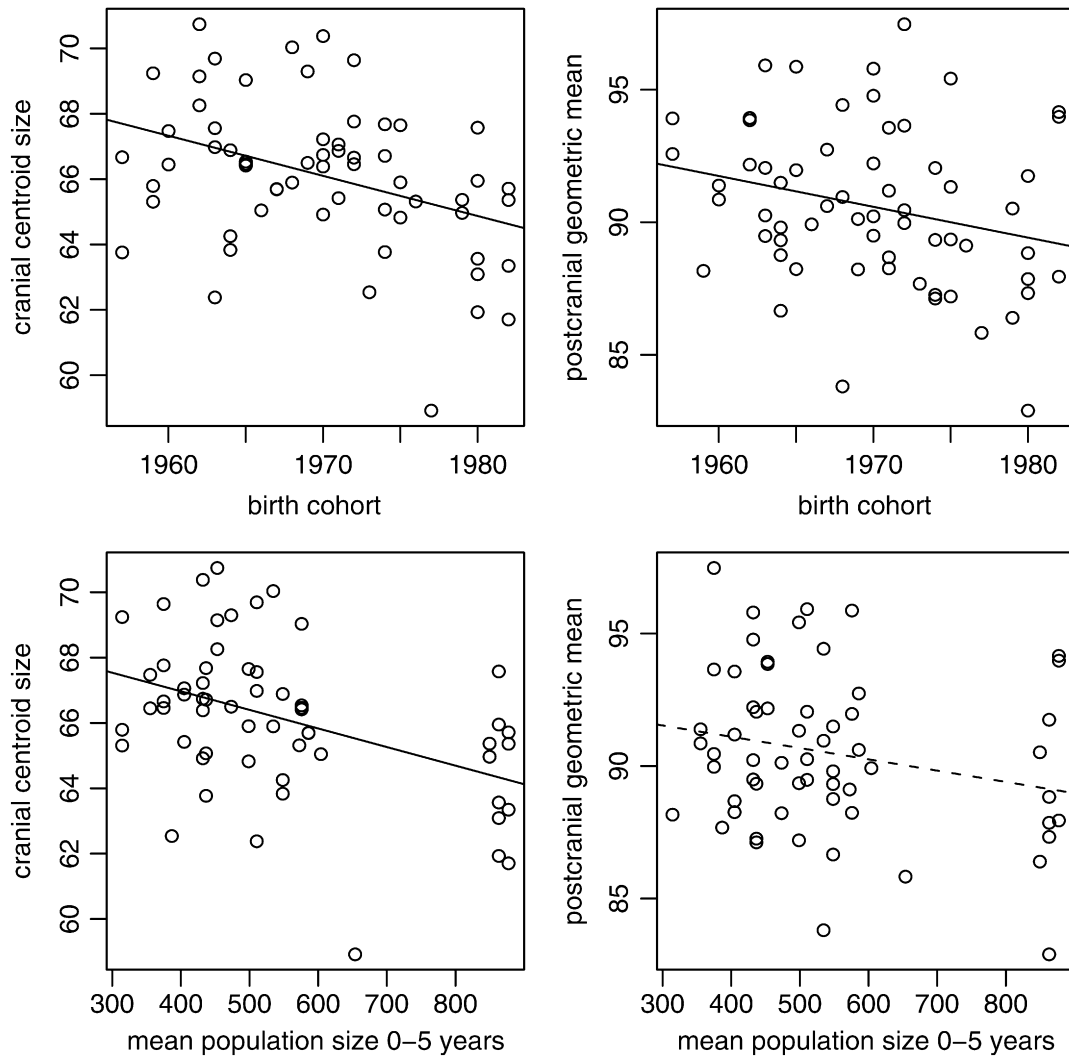


Figure 2. Temporal or density-related size trends in scatterplots of cranial centroid size or postcranial geometric mean on birth cohort or average population size for the first six years of life. Solid lines indicate significant regressions (Table 4).

animals have found similar patterns of temporal change in opposition to directional selection (Merila et al., 2001a,b; Reale et al., 2003a,b; Charmantier and Garant, 2005; Wilson et al., 2007). Decline in other measures of health would be consistent with the crowding explanation for size reduction. Health changes have been explored in the skeletal Cayo Santiago sample but this has largely centered on contrasting individuals that grew up before and after the resumption of regular provisioning of the colony in the mid-1950s. DeRousseau and Reichs (1987) showed size increases and some changes in body proportions between these periods while Guatelli-Steinberg and Benderlioglu (2006) recently illustrated nutritional stress events, recorded in linear enamel hypoplasias, were more common in the pre-provisioning period.

Density effects on growth could also be related to female age of first reproduction. However, we found no relationship between age of first reproduction and either skeletal size measurement in our sample (results not reported). This may be due to opposing effects of curtailment of size increase by early reproduction and increased likelihood of earlier reproduction in females that have reached a given size threshold and were larger at earlier ages (Stearns and Koella, 1986; Day and Rowe, 2002). Nor did we find any relationship between female matriline social rank and cranial or postcranial size (cf. Bercovitch and Berard, 1993).

Fourth, it is possible the female skeletons available for analysis are not representative of the population as a whole. Fifty-five females is admittedly a small sampling of the colony in which 489 females were born in the accepted cohorts and lived to ages past 6.5 years. However, as long as the females that were measured—the maximum available in the skeletal collection—are a random sample of the 191 adult females that remained on the island until death from natural causes, standard statistical procedures should produce valid regression statistics which we interpreted as selection differentials or gradients (Little and Rubin, 2002). However, the temporal decline in size could have resulted from removal of animals for colony management. For females born over the 1957–1982 period, only 39% of females living to ages over 6.5 years actually remained on the island throughout their entire life until death by natural causes. Any bias toward removal of larger females could overwhelm the selection patterns documented in the remaining fraction of the population. Similar arguments could be made about selection or temporal trends in male size. Indeed, patterns of selection on males may be particularly important given that genetic correlations between the sexes are often very strong (Lindénfors, 2002; Gordon, 2006a).

Finally, adult osteological changes might have influenced the selection gradients or differentials. Drawing on a similar Cayo Santiago sample, Wang et al. (2006a,b, 2007) suggested that the cranium

of adult female macaques could continue to grow up to as late as 15 years old, based on the age at death–cranial size relationship and the fact that cranial sutures remain open on many skulls to these late ages (cf. Falk et al., 1989). Jones et al. (2000) suggested a similar pattern in adult male howler monkeys, but not females. To limit the potential impact of growth later in adulthood, we restricted our cranial size measurements to regions previously shown to undergo little change in later years. While there is the potential for continued adult growth when sutures remain open, it does not demonstrate that adult growth occurs. Some human cranial sutures in known age at death samples remain open in modest frequencies well past 35 years (McKern and Stewart, 1957; Sahni et al., 2005). Fundamentally, cross-sectional samples cannot adequately distinguish between these possibilities in the cranium. Unfortunately, longitudinal studies of macaque cranial growth terminate in young adulthood and have been confined to the face (Schneiderman, 1992; Koppe et al., 1999). The only longitudinal radiographic studies of cranial change during adulthood are of humans. The amount of change between repeated measurements on the same subject in these studies is typically <3% (Tallgren, 1974; Behrents, 1984), which is much smaller than skeletal changes implied by the selection gradients or differentials.

Furthermore, none of these studies have addressed continued adult growth in the postcranium, where similar selection differentials are found. While postcranial growth in the bones we measured terminates in early adulthood with epiphyseal fusion, postcranial measurements could be influenced by increasing susceptibility to arthritic joint diseases. This was explored in a Cayo Santiago skeletal samples by Rothschild et al. (1999, 1997), who showed that bony overgrowth of the joint surface increased in frequency with age (15% 8 years, 22% 12 years), most often in the wrist and knee. Because these overgrowths are almost exclusively around the periphery of the joint, their potential impact on measurement of length is minimal. Assessment (by JET) of postcranial joint pathology in our sample confirms this, and excluding individuals with notable pathologies ($N = 14$) had very minor numerical effects on the regression results.

In summary, although there are alternative interpretations of the skeletal size–fitness relationship in the Cayo Santiago females, we consider them to be very unlikely. Selection for large body size is consistent with the many potential advantages of large size for female mammals (Ralls, 1976; Smuts, 1987; Martin, 1996; Isaac, 2005). Nevertheless, how size influences life history, physiology, and behavior to yield longer lifespans at Cayo Santiago is not yet clear, nor are the causes for the simultaneous decline in female skeletal size.

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