Primate Population Studies at Polonnaruwa. II. Heritability of Body Measurements in a Natural Population of Toque Macaques (*Macaca sinica*)

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The heritability of quantitative traits, or the proportion of phenotypic variation due to additive genetic or heritable effects, plays an important role in determining the evolutionary response to natural selection. Most quantitative genetic studies are performed in the laboratory, due to difficulty in obtaining genealogical data in natural populations. Genealogies are known, however, from a unique 20-year study of toque macaques (*Macaca sinica*) at Polonnaruwa, Sri Lanka. Heritability in this natural population was, therefore, estimated.

Twenty-seven body measurements representing the lengths and widths of the head, trunk, extremities, and tail were collected from 270 individuals. The sample included 172 offspring-mother pairs from 39 different matrilineal families. Heritabilities were estimated using traditional mother-offspring regression and maximum likelihood methods which utilize all genealogical relationships in the sample.

On the common assumption that environmental (including social) factors affecting morphology were randomly distributed across families, all but two of the traits (25 of 27) were significantly heritable, with an average heritability of 0.51 for the mother-offspring analysis and 0.56 for the maximum likelihood analysis. Heritability estimates obtained from the two analyses were very similar. We conclude that the Polonnaruwa macaques exhibit a comparatively moderate to high level of heritability for body form. © 1992 Wiley-Liss, Inc.

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INTRODUCTION

Quantitative genetic theory has had a large impact on evolutionary biology over the past ten years and this has spurred interest in genetic analyses of complex characters in natural populations. Evolutionary biologists have realized that the

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evolutionary response to selection depends directly on the extent and pattern of heritable variation in addition to the pattern of selection [Falconer, 1981]. Patterns of heritable variation can modify both the rate and direction of evolution, steering it away from the optimal evolutionary path defined by selection [Lande, 1979; Cheverud, 1984]. By necessity, most measures of heritable variation are obtained in a laboratory environment, due to the need for genealogical data on the individuals included in the sample. However, the validity of generalizing the results from such studies to natural populations remains an open question [Mitchell-Olds & Rutledge, 1986; Riska et al., 1989].

Studies of heritable variation in morphological and life history characters are particularly difficult to carry out in natural primate populations because longterm studies are required to produce the necessary genealogical database. Thus, the long-term study of behavior, ecology and demography of toque macaques (*Macaca sinica*) at Polonnaruwa, Sri Lanka [Dittus, 1977a, 1988] provides a rare opportunity to estimate quantitative genetic parameters in a natural population of primates.

In this report, we analyze the heritability of a series of body measurements reflecting the lengths and widths of limb segments, tail, trunk, and head. Body form, especially the relative lengths of tail and trunk, has played an important role in macaque systematics [Hill, 1974; Fooden, 1976] and is quite divergent among species. The extent of genetic variation in these characters is important in providing a basis for the evolutionary divergence and adaptation of body form in macaques. The genetic analysis of these characters will also provide an estimate of levels of heritable morphological variation in a natural primate population. Such estimates are entirely lacking for nonhuman primates. Estimates obtained from captive colonies can then be compared with the natural situation.

We will also test for a pattern of heritability often described for body measurements. Osborne and DeGeorge [1959] suggested that measurements taken along the longitudinal axis of the body will tend to be more highly heritable than measurements of body widths and circumferences. This suggestion has often been supported in studies of human body measurements [see Devor et al., 1986a,b] but has rarely been tested in other species.

METHODS

The population of toque macaques living in the Nature Sanctuary and Archeological Reserve at Polonnaruwa, Sri Lanka has been the subject of a long-term study by W. Dittus. Continuous observations of the population have been made from September 1968 to May 1972 and again from March 1975 to 1991. Intermittent observations were made from May 1972 to March 1975. The natural dry evergreen forest that the macaques inhabit, as well as several aspects of macaque ecology, behavior, and demography have been described earlier [Dittus, 1977a,b, 1979, 1986, 1988].

The population consists of approximately 600 macaques distributed among 23 social groups. All macaques in the population were individually identified by methods described in Dittus and Thorington [1981]. Censuses of each group were made once a month. During the birth season individual females were observed every one to five days in order to obtain accurate birth dates. Demographic events (birth, death, emigration) were recorded for each individual macaque.

Matrilineal relationships were based exclusively on known births. Paternity is unknown. As shown by Konigsberg and Cheverud in this volume, restriction to matrilineal kin should not result in biased heritability estimates. Chronological ages for individual macaques were obtained from known birth dates. Ages of in-

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	Mother- offspring heritability	Р	Maximum likelihood heritability (SE)	Р	Phenotypic variance (cm ²)
Crown-rump length	0.53	0.004	0.58 (0.102)	0.00005	2.922
Occiput to tail base	1.04	0.002	0.99 () ^a	0.00001	4.632
Trunk length (ventral)	0.90	0.002	0.97 (0.092)	0.00001	2.651
Abdominal circumference	0.21	0.028	0.28 (0.093)	0.01050	4.099
Thoracic circumference	0.44	0.002	0.52 (0.106)	0.00012	1.830
Biacromial width	0.23	0.080	0.38 (0.115)	0.00721	0.644
Bitrochanteric width	0.26	0.040	0.35 (0.169)	0.05510	0.278
Arm circumference	0.96	0.002	0.99 (—) ^a	0.00001	0.886
Arm length	0.49	0.006	0.49 (0.114)	0.00110	0.427
Forearm length	0.39	0.008	0.50 (0.131)	0.00530	0.472
Hand length	0.18	0.094	0.38 (0.113)	0.01007	0.224
Hand width	0.56	0.002	0.62 (0.081)	0.00001	0.029
Calf circumference	0.77	0.002	0.73 (0.083)	0.00001	0.611
Thigh circumference	0.91	0.002	0.88(0.082)	0.00001	2.283
Thigh length	0.40	0.004	0.44 (0.110)	0.00292	0.570
Leg length	0.66	0.002	0.68 (0.111)	0.00012	0.709
Foot length	0.47	0.002	0.46 (0.092)	0.00021	0.251
Foot width	0.26	0.040	0.35 (0.095)	0.00326	0.028
Tail length	0.67	0.002	0.67 (0.085)	0.00001	12.513
Head length	0.64	0.002	0.58 (0.120)	0.00016	0.111
Head breadth	0.39	0.004	0.48 (0.105)	0.00046	0.082
Biorbital width	0.82	0.002	0.86 (0.072)	0.00001	0.051
Bizygomatic width	0.53	0.006	0.47 (0.097)	0.01699	0.187
Bigonial width	0.68	0.002	0.68 (0.076)	0.00001	0.262
Upper facial height	0.25	0.018	0.45 (0.133)	0.00716	0.051
Lower facial height	-0.21	0.066	0.00 (0.078)	0.50000	0.063
Nasal width	0.08	0.166	0.26 (0.096)	0.03260	0.021

 TABLE I. Heritability of Body Measurements in the Polonnaruwa Toque Macaques as

 Estimated With Mother-Offspring Regression and Maximum Likelihood Methods*

*Probabilities for mother-offspring analysis were estimated with randomization tests while probabilities for maximum likelihood estimates were obtained from standard likelihood ratio tests. The phenotypic variance estimate presented was obtained from the maximum likelihood analysis.

^aStandard errors could not be calculated because the heritability estimates reached the upper bound.

dividuals born before 1968 were estimated based on correlations between morphological development and age derived from known-age individuals in this population [Dittus, 1988]. At this point in time, birth dates are known for most animals living in the population.

Over the last three years the macaques at Polonnaruwa have been systematically trapped by social group (and released unharmed) in order to collect genetic, morphological, and a variety of biomedical data on the population. A series of 27 measurements were taken in the field with an anthropometer, calipers, and flexible steel tape on each animal trapped. These measurements included various trunk lengths, widths, and circumferences, arm and leg segment lengths and circumferences, and various head lengths, breadths, and heights (see Appendix and Table I). Up to this time, data have been collected on 270 animals in 13 social groups.

Measurements were made by W. Dittus on about one-half of the social groups and by research assistants on the remainder. For all observers, measurements were practiced on several test animals in order to establish both intra- and inter-

observer replicability and consistency. This task mainly involved learning to make minor adjustments in the placement of calipers at specific points on different anatomical structures (condyles, grooves, distal margins) used as anchors for measurement. Difficult landmarks, such as the distal margins of rounded condyles, often were measured several times in an animal until a consistent measure was achieved. Skeletal widths and lengths of fixed or non-articulated segments showed the least error. The effect of small error in measuring over articulated segments, such as crown-rump length, was least where these segments were very long. Most error probably involved abdominal circumferences where gut contents may have contributed to the variation. The observations were visually screened for outliers after data collection was completed using plots of measurement on age separately for each sex. Outliers were set to missing values prior to analysis. Approximately 0.2% of the data was set to missing for exhibiting outlying values.

Age- and sex-specific samples needed to be combined to obtain sufficient sample sizes for genetic analysis. Thus, prior to estimating heritabilities, age- and sex-related variation was removed from the data. This was accomplished by first fitting a spline curve to the age distribution for individual traits, separately by sex. Spline curves provide local fits to bivariate frequency distributions by tracking through the middle of the data distribution. The algorithm used was provided by D. Schluter [1988]. Inspection of these curves indicated a tri-linear model for growth in all characters, with an early growth phase from 0 to 2.5 years, followed by a second period of slower growth which was sexually dimorphic in both rate and age of completion, and, finally, the period of adulthood after growth had ceased. The length of the second growth period varied by trait [Cheverud et al., in press]. The trait- and sex-specific growth period intervals were detected by visual inspection of the splines. Linear regressions were fit to the data for each of the three periods separately by sex for each character. The residuals from these regressions, now free of age- and sex-related variation, were used for analysis of heritability. The use of age- and sex-corrected data will bias heritability estimates slightly downward, to the extent that the genetic correlation between the sexes deviates from one [Lande, 1980] and to the extent that juvenile and adult realizations of a trait have genetic correlations less than one [Cheverud et al., 1983].

Quantitative genetic estimates were obtained using the standard model [Falconer, 1981] in which a phenotypic value is considered as the sum of an additive genetic, or breeding, value (A) and an environmental deviation (E), which also contains the non-additive genetic (dominance and epistasis) effects,

$$\mathbf{P} = \mathbf{A} + \mathbf{E}.\tag{1}$$

Assuming no genotype x environment covariance, the phenotypic variance (V_P) can be decomposed into an additive genetic variance (V_A) and an environmental variance (V_E) ,

$$\mathbf{V}_{\mathbf{P}} = \mathbf{V}_{\mathbf{A}} + \mathbf{V}_{\mathbf{E}}.$$
 (2)

Heritability (h^2) is the proportion of phenotypic variance due to additive genetic effects,

$$h^2 = V_A / V_P. \tag{3}$$

Thus, heritability measures the proportional contribution of inheritance to interindividual differences. Natural selection produces evolution through the selection of heritable variation, so the magnitude of the heritability determines the rate of evolution in combination with the strength of selection [Falconer, 1981]. Heritabilities for these 27 measurements were estimated using the regression of offspring on mother and using maximum likelihood methods [Shaw, 1987; Konigsberg & Cheverud, 1991]. In mother-offspring analysis, heritability is twice the regression of offspring phenotype on maternal phenotype, since the covariance of mother and offspring is half the additive genetic variance [Falconer, 1981]. There were 172 offspring-mother pairs from 32 different matrilineages included in the sample. It should be noted that mother-offspring pairs encompassed both adult and juvenile offspring of mothers.

Estimating heritabilities from similarities among relatives assumes that the population is in Hardy-Weinberg and linkage equilibrium and that environments are randomly distributed among individuals rather than being concentrated in families. To the extent that familial environment causes morphological similarity among family members, heritabilities will be overestimated. Potentially important sources of familial environment in macaques are maternal dominance rank and social group rank. Both within- and between-group ranks are important for access to resources [Dittus, 1977a, 1986] and thus could cause morphological similarity among family members. Additionally, we assume autosomal inheritance and note that heritability estimates may be biased downwards if the environment differs across generations.

Appropriate analytical tests of significance for offspring on mother regressions are difficult to derive and are based on assumptions of multivariate normality and independence of cases. In natural populations these assumptions will rarely, if ever, be met due to a lack of independence among the mother-offspring pairs in the sample. Mothers have multiple offspring; may often be sisters, daughters, or grandmothers of others in the sample, and thus are not independent. For this reason, standard significance tests are inappropriate for mother-offspring analyses of primate populations.

Therefore, we estimated the statistical significance of mother-offspring-based heritability values using a randomization test. This test assumes only that each random assignment of offspring to mothers is equally likely. In a randomization test, the offspring are repeatedly and randomly assigned to mothers and heritabilities estimated from the randomized data. This provides a distribution of offspring-mother regressions expected under the null hypothesis of no heritability. The observed value is then compared with this simulated distribution and the proportion of simulated heritabilities greater than or equal to the observed value is taken as the probability of observing such an extreme value when there is, in fact, no heritability for the character in the sample analyzed [Cheverud et al., 1990; Edgington, 1987]. Five hundred iterations were used to estimate the null distribution.

Heritabilities were also estimated using maximum likelihood pedigree methods [Shaw, 1987]. The major advantage of maximum likelihood approaches in quantitative genetics is that all of the animals and types of relationship in the population can be jointly utilized in estimating heritability. The mother-offspring analysis ignores other kinds of relationship, such as half-sibs, grandmother-grandchild, and aunt-niece. The inclusion of this additional information in maximum likelihood estimation can help provide more accurate estimates of heritability, given that the assumptions noted above for the mother-offspring analysis also hold for the other forms of relationship. The maximum likelihood methods also allow standard errors to be estimated for the heritabilities.

Potential disadvantages of using the maximum likelihood pedigree approach in this study, in contrast to the mother-offspring analysis, include the errors in measuring genetic relationships between individuals from genealogical informa-

tion restricted to the maternal line and the possibility of greater environmental similarity among relatives. For example, it is possible that sibs share familial environments more extensively than relatives across generations, thus biasing heritabilities upwards relative to those obtained from mother-offspring analysis. Another disadvantage of maximum likelihood techniques is that both estimation and significance testing rely on assuming a normal distribution. The motheroffspring analysis avoided the assumption of normality for both estimation and significance testing. However, the traits used here did not depart from normality to a significant degree.

The likelihood approach applied here is described in some detail by Konigsberg and Cheverud [1991] and was carried out using modifications of the MAXLIKH2 program obtained from L. Konigsberg. The likelihood maximized is that suggested by Hopper and Matthews [1982] and Lalouel's [1979] search procedure was implemented to identify the maximum likelihood. Potential heritability estimates were limited to the theoretically permissible range between 0.00 and 1.00. The procedure identifies the mean, phenotypic variance, and level of heritability which provide the best fit to the observed trait values given their distribution with respect to genealogical relationships by an iterative search of the parameter space. Heritabilities estimated in this way were tested for statistical significance using standard likelihood ratio tests comparing the likelihood of a model estimating only the mean and variance (assuming no heritability) with a model estimating all three parameters [Shaw, 1987]. Standard errors for these heritability estimates are also available.

RESULTS

Offspring-mother regressions were obtained for each of the 27 traits (see Fig. 1 and Table I). Twenty-three of the 27 heritabilities, or 85% of them, are significantly different from zero at the 5% level. The heritability estimates range from -0.21 (lower facial height) to 1.04 (occiput to tail base; see Fig. 1) with an average of 0.51. The two estimates outside of the permissible 0.00 to 1.00 range are not significantly outside the theoretical limits and represent a common finding for studies with multiple characters [Cheverud, 1988].

Maximum likelihood heritability estimates ranged from 0.00 to 1.00 and all but two traits, bitrochanteric width and lower facial height, show statistically significant heritabilities at the 0.05 level using the likelihood ratio test (see Table I). These heritability estimates averaged 0.56 and, as a group, were significantly higher than the mother-offspring estimates (Wilcoxon signed-rank test; P =0.004). The largest differences tended to be for those traits exhibiting low heritability estimates (h² < 0.30) in the mother-offspring analysis. The Spearman rank order correlation of mother-offspring with maximum likelihood heritability estimates was very high ($r_s = 0.96$). Additive genetic variances can be obtained by multiplying the heritability by the maximum likelihood estimate of phenotypic variance given in Table I. Overall, both heritability estimation methods provide strong evidence for heritable variation in body form in the Polonnaruwa population of toque macaques.

The pattern of heritability for these characters was also investigated. Only the results obtained from the maximum likelihood estimates will be described here because of the high correlation between results of the mother-offspring and maximum likelihood analyses. Trunk, limb (including tail), and head measurements did not significantly differ in heritability (average $h^2 = 0.58$, 0.60, and 0.47, respectively). Neither did length measurements relative to circumferences and widths (average $h^2 = 0.55$ and 0.56, respectively). Inspection of the heritabilities,



Fig. 1. Mother-offspring regression for occiput to base of tail. The slope of the least squares regression and its 95% confidence interval are drawn. Heritability is estimated as twice the slope of the regression. Note that the least squares slope, which is estimated by minimizing the residuals for the dependent variable alone, does not pass through the middle of the data scatter. The major axis of the data, which minimizes residuals orthogonal to the regression line would have a higher slope, but would not correspond to the theoretical relationship from which heritabilities are estimated (Falconer, 1981).

however, suggested that within the trunk, lengths had higher heritabilities than widths and circumferences ($h^2 = 0.85$ vs. 0.38). In contrast, in the limbs circumferences (but not widths) had higher heritabilities than length measurements ($h^2 = 0.87$ vs. 0.51). Both of these contrasts are statistically significant using Mann-Whitney U tests.

DISCUSSION

The results of our analyses suggest significant heritable variation for morphological characters in the Polonnaruwa toque macaques. However, the analysis assumes that environmental factors affecting morphology are randomly distributed with respect to family membership. Since family members may share similar environments, which differ among families, heritability may be overestimated. Future analyses measuring the effects of shared familial environments on morphology will indicate the extent to which heritabilities may be overestimated.

Notwithstanding this limitation, identical assumptions had been made in the analysis of heritable variation for skeletal characters in the rhesus macaque population on Cayo Santiago [Cheverud & Buikstra, 1982] and in animal populations in general [Mousseau & Roff, 1987]. The estimated 50-55% heritable variation of morphological characters for the toque macaques at Polonnaruwa exceeds the 30% found in the rhesus macaques of Cayo Santiago [Cheverud & Buikstra, 1982; Konigsberg & Cheverud, 1991], and is at the high end of the range found by Mousseau and Roff [1987] in their general survey of heritability for morphological characters in animals. The results therefore suggest that a relatively high proportion of phenotypic variation is inherited in the Polonnaruwa population compared with other animal populations.

Heritability estimates were obtained from both mother-offspring and maximum likelihood pedigree methods. The estimates obtained are quite similar, as we expected, due to the fact that the samples of relatives used in each analysis overlap to a considerable extent. With regard to the similarity of estimates obtained from these two methods, our findings are similar to those of Konigsberg and Cheverud [1991] for craniometric traits in the Cayo Santiago rhesus macaques.

In general, the pattern of heritability did not fit that hypothesized by Osborne and DeGeorge [1959] and often observed in human populations, with heritabilities of length measurements exceeding those estimated for widths and circumferences [Devor et al., 1986a,b]. Body length measurements were only significantly more heritable than body widths and circumferences in the trunk. The opposite pattern, circumferences more highly heritable than lengths, was observed in the limbs. Instead, some of the variation in heritability estimates may be due to differences in repeatability (or measurement error) among measurements. The repeatability (proportion of observed variance which is between subjects rather than being due to measurement error) sets an upper limit on heritability [Falconer, 1981], so that measurements with relatively low repeatabilities (high degrees of measurement error) will also tend to have relatively low heritabilities. Measurement error may have contributed to relatively low heritabilities for trunk circumferences and widths due to variations caused by breathing and stomach contents. Other measurements exhibiting relatively low heritabilities, such as nasal width, lower and upper facial height, and hand and foot measurements, tend to have relatively low repeatabilities in human anthropometric studies [Spielman et al., 1972; Jamison & Zegura, 1974]. Thus, much of our variation in heritability may be due to variation in the accuracy with which different measurements can be recorded.

Heritability estimates are population specific and may change with changes in allele frequencies and/or changes in environmental factors. Thus, extrapolation of these results to other populations must be considered speculative. However, to the extent that the levels of heritable variation discovered here can be generalized [Falconer, 1981], there appears to be little general genetic constraint on body form adaptation and diversification among macaques. Systematic studies of macaques have indicated significant interspecific differences in body size and tail length [Hill, 1974; Fooden, 1976]. These differences are likely to be local adaptations to the physical environment [Fooden, 1976]. Our general results indicate adequate genetic variation for a quick response to selection on body size and tail length. However, multivariate analyses must be undertaken to determine the levels of heritable variation for particular combinations of body measurements. While morphology is generally heritable in this population, certain body shapes (character combinations) may still show limited genetic variation. Also, it is possible that results may vary from population to population and species to species. Studies on other macaque populations would be useful in evaluating the generality of the results presented here.

Our results indicate that this population would respond to natural selection on body form. Accepting that the opportunity for selection is highest in those lifestages and subpopulations that are subject to high mortality, selection on body size and shape might be particularly intense for migrating subadult males [Dittus, 1977a]. In the future, continued collection of demographic records and morphometrics will allow measurements of selection on morphological characters (covariance of survival and reproductive success with morphology) and prediction of expected evolutionary responses.

The finding of significant heritable variation in this population is the first such finding for a natural nonhuman primate population and will provide one of the few opportunities to study inheritance and selection concurrently in a natural setting. Indeed, it is a rare natural study in mammalian genetics and raises a wealth of possibilities for studying the effects of natural selection on morphological features and the population genetic structure of morphological characters in macaques [Cheverud, 1981].

CONCLUSIONS

1. There is a relatively high degree of heritable variation for body measurements in the toque macaques at Polonnaruwa, Sri Lanka. This result depends, in part, on the assumption that environmental factors affecting morphology are randomly distributed with respect to genealogical relationship.

2. Heritability estimates obtained from mother-offspring analysis and maximum likelihood estimates based on all genealogical data are quite similar.

3. In contrast to findings in human anthropometric studies, measurements along the longitudinal axes of the body are not more highly heritable than measurements of body widths and circumferences. Instead, the relatively lowly heritable measurements may exhibit low heritabilities due to relatively high measurement error.

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