

Effects of Inbreeding on Infant Mortality in Captive Primates

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Received May 26, 1981; revised December 14, 1981

*Breeding records for 16 primate colonies representing six families and both suborders were obtained from 10 institutions breeding primates in captivity and from the international studbook on one endangered species. Inbreeding coefficients relative to the founding population were calculated for each individual born. Individuals with an inbreeding coefficient of zero were classified as "noninbred"; those with inbreeding coefficients greater than zero, as "inbred." Infant mortality was defined as all deaths prior to the age of 6 months. Infant mortality of inbred young was higher than that of noninbred young in 15 of the 16 colonies surveyed ($P = 0.0003$, one-tailed sign test). The higher mortality rate of the inbred young was significant by a Fisher's exact test with a probability less than or equal to 0.05 in five of the individual colonies: *Lemur fulvus*, *Saguinus fuscicollis illigeri*, *Saguinus fuscicollis*, *Leontopithecus rosalia*, and *Mandrillus sphinx*.*

KEY WORDS: inbreeding; infant; mortality; primates; genetics.

INTRODUCTION

The annual importation of wild primates into the United States for biomedical and other purposes has decreased steadily during the 1970s, from 91,000 at the beginning of the decade to less than 24,000 at the end (Muckenhirn, 1975; Mack, 1980). Efforts to breed primates in captivity

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have increased during this period but by 1978 only 5093 primates were produced in 31 of the major private and public laboratories (Gerone, 1978). This number represents only about 15% of the estimated 32,000 to 34,000 primates of the most common 10-15 species needed annually for biomedical requirements (Department of Health, Education and Welfare, 1978; Held, 1980). The limited numbers of wild-caught individuals that were used to establish breeding colonies in many species, together with management practices that resulted in skewed sex ratios reaching one male to eight females (Gerone, 1978; Smith, 1980), have resulted in inbreeding in captive colonies.

Inbreeding has repeatedly been shown to result in loss of vigor, decreased fertility, and increased juvenile mortality in laboratory (Wright, 1977; Festing, 1979), domestic (Lasley, 1978), and zoo animals (Slatis, 1960; Flesness, 1977; Bouman, 1977; Ralls *et al.*, 1979). Deleterious effects have also been documented in humans (Cavalli-Sforza and Bodmer, 1971; McKusick, 1978; Schull and Neel, 1972).

The effects of inbreeding on nonhuman primates have been documented by Packer (1979) for *Papio anubis* and Crawford and O'Rourke (1978) and O'Rourke (1979) for *Papio hamadryas*. Packer noted that the offspring sired by a *Papio anubis* who had transferred into a group containing related females suffered a higher than normal rate of infant mortality. Studies on a captive *Papio hamadryas* colony indicated that inbred baboons were at a greater risk of contracting lymphoma (Crawford and O'Rourke, 1978), in addition to exhibiting lower mean values of anthropometric measurements (O'Rourke, 1979), than noninbred baboons.

Smith (1980) calculated the theoretical effects of the age and sex composition of six captive groups of *Macaca mulatta* at the California Primate Research Center upon level of inbreeding and infant mortality and found that these effects were likely to be substantial. Although he recommended that colony management be modified to reduce inbreeding, he presented no actual data on the effects of inbreeding on infant mortality in nonhuman primates. The Wisconsin Regional Primate Research Center has already initiated efforts to minimize inbreeding in their rhesus macaque colony (Curie-Cohen, 1981). We report here on the relationship between inbreeding and infant mortality in 16 colonies of captive primates representing six families and both suborders.

METHODS

Data on 16 colonies of primates (Table I) were compiled from the breeding records of 10 institutions and the international studbook for

Cercopithecoidea

<i>Macaca nemestrina</i>										
(pig-tailed macaque)										
Lived	1185	21								Seattle Regional Primate Research Center
Died	869	15								
% Mort	42.3	41.7								
<i>Macaca fascicularis</i>										
(crab-eating macaque)										
Lived	142	21								New England Regional Primate Research Center
Died	64	10								
% Mort	31.1	32.3								
<i>Macaca mulatta</i>										
(rhesus macaque)										
Lived	25	8								Wisconsin Regional Primate Research Center
Died	0	2								
% Mort	0.0	20.0								
<i>Macaca nigra</i>										
(celebes black ape)										
Lived	52	5								Oregon Regional Primate Research Center
Died	23	6								
% Mort	30.7	54.5								
<i>Mandrillus sphinx</i>										
(mandrill)										
Lived	8	5								New York Zoological Park (Bronx Zoo)
Died	0	18								
% Mort	0.0	78.3								
Pongidae										
<i>Pan troglodytes</i>										
(chimpanzee)										
Lived	160	14								Yerkes Regional Primate Research
Died	67	6								
% Mort	29.5	30.0								

^aFor sign test, + indicates inbred juvenile mortality higher than noninbred juvenile mortality ($P = 0.0003$).

^cSome authorities consider these taxa to be subspecies of *Lemur macaco* (Napier and Napier, 1967).

^dBecause of the distribution of such small samples within the cells and the empirical marginal splits, there is no possibility of a significant outcome. In such circumstances no "test" could be performed since only one outcome is possible (n/a, not applicable).

*Significant at the 0.01 level, Fisher's exact test.

**Significant at the 0.05 level, Fisher's exact test.

golden lion tamarins (*Leontopithecus rosalia rosalia*) (Kleiman, 1980). Data on parentage, date of birth, date of death or removal, and cause of death (natural or experimental) were recorded for each individual used in the study.

The computer program COEF (MacLean, 1969) was used to calculate inbreeding coefficients as devised by Sewall Wright (1922) for each individual. Each individual was classified as "inbred" or "noninbred" and as having "lived" or "died." Individuals with an inbreeding coefficient of zero were classified as noninbred; those with inbreeding coefficients greater than zero were classified as inbred. Founding individuals were assumed to be unrelated to each other and individuals subsequently added to the colonies were assumed to be unrelated to the existing population unless exact relationships were known. This assumption is probably untrue in some instances. However, the resulting error would be the classification of some inbred infants in the noninbred group. If inbred infants have a higher mortality rate than noninbred infants, this would tend to increase the mortality rate of our noninbred group and thus decrease the probability of our finding a higher mortality rate in inbred animals. In some cases it was not possible to determine which of two or more males present in a group had sired an offspring. If all the males present were unrelated to the mother of the individual, the offspring was classified as noninbred. If both related and unrelated males were present, the offspring was excluded from the study. Descendants of excluded individuals were also excluded unless they could be classified as inbred on the basis of subsequent breeding records. In these instances the individuals were known to be inbred regardless of the status of their ancestors with unknown sires. The inbreeding coefficients calculated for such individuals may be underestimates because they are based on the assumption that the ancestors with unknown sires were not inbred. However, because we did not distinguish between different degrees of inbreeding when comparing inbred and noninbred mortality rates, such underestimates would not affect our overall results.

Infant mortality rates for inbred and noninbred young were calculated for each colony. Infant mortality was defined as all deaths prior to the age of 6 months. Offspring surviving to that age were considered to have "lived"; all others, including premature births and stillbirths, if recorded, and accidental deaths, which should be distributed between inbred and noninbred young in a statistically random manner, were included under "died." Individuals who were transferred to other institutions and whose status at the age of 6 months was unknown as well as individuals who were killed before 6 months of age for research purposes were excluded from the study.

For all groups except the rhesus macaques (*Macaca mulatta*), all births since the founding of the colony were surveyed and offspring born within

the 6 months prior to the most recent entry in the pedigree were excluded; these offspring could not be reliably classified as having lived or died since they were under 6 months of age. Table II contains, for each colony, the first and last births used in the study; the total number of births during that period; the number of births that were excluded because of research-related deaths prior to 6 months of age, unknown status, or unknown parentage; and the number of births used in the study.

The Wisconsin Regional Primate Research Center provided us with only the data for those rhesus macaque family groups that included both inbred and noninbred young. Data from seven family groups, comprising a total of 25 noninbred and 10 inbred offspring, were combined to give inbred and noninbred infant mortality rates.

Data on the yellow baboon (*Papio cynocephalus*) colony at the Seattle Regional Primate Research Center and the rhesus macaque colony at the Oregon Regional Primate Research Center were also analyzed but too few inbred births were found to permit a comparison of infant mortality rates in inbred and noninbred animals. Many breeding facilities are currently maintaining macaques in large outdoor groups with many breeding-age males. Since the sires of the young are unknown in such colonies, an analysis of the breeding records was not possible.

RESULTS

Infant mortality rates in inbred and noninbred young, mean inbreeding coefficients of the inbred young, and the frequency distribution of the inbreeding coefficients for each species are shown in Table I. Although several colonies (*Galago crassicaudatus argentatus*, *Ateles fusciceps robustus*, *Saguinus fuscicollis illigeri*, and *Macaca fascicularis*) have average inbreeding coefficients at or above the 0.25 level, which is equivalent to father-daughter, mother-son, or full-sibling matings, most of the colonies surveyed exhibited average inbreeding coefficients less than this. Infant mortality of inbred young was higher than that of noninbred young in 15 of the 16 colonies surveyed. This trend was highly significant by a one-tailed sign test ($P = 0.0003$). The only exception was the pig-tailed macaque (*Macaca nemestrina*) colony at the Seattle Regional Primate Research Center. The higher mortality rates of the inbred young were significant by a Fisher's exact test with a probability less than or equal to 0.05 in five of the individual colonies: the brown lemur (*Lemur fulvus*), Illiger's saddle-back tamarin (*Saguinus fuscicollis illigeri*), the saddle-back tamarin (*Saguinus fuscicollis*), the golden-lion tamarin (*Leontopithecus rosalia rosalia*), and the mandrill (*Mandrillus sphinx*).

Table II. Pedigree Data for Colonies Surveyed

Colony	Date of the first birth in pedigree	Date of the last birth used	No. of births during this period	No. of births excluded	Births used in study
Ring-tailed lemur	2/14/64	11/12/78	100	24	86
Black lemur	9/04/66	9/07/78	41	0	41
Brown lemur	1/30/64	3/26/78	141	9	132
Greater galago	3/18/64	11/28/78	201	11	190
Melanotic galago	8/26/64	4/24/78	52	0	52
Squirrel monkey	9/16/74	9/10/79	488	38	450
Black spider monkey	4/26/66	9/11/79	23	0	23
Illiger's saddle-back tamarin	5/14/70	2/08/80	245	12	233
Saddle-back tamarin	11/25/69	5/22/80	416	10	406
Golden lion tamarin	7/07/58	12/31/79	599	85	514
Pig-tailed macaque	1/02/60	3/05/79	3050	960	2090
Crab-eating macaque	7/09/69	5/14/79	335	98	237
Rhesus macaque	4/08/66	6/30/79	37	2	35
Celebes black ape	10/09/62	3/01/79	97	11	86
Mandrill	8/05/60	8/01/79	40	9	31
Chimpanzee	9/11/30	12/23/78	288	41	247

The size of the difference between inbred and noninbred infant mortality rates varied considerably across colonies; the differences in the crab-eating macaque (*Macaca fascicularis*) colony at the New England Regional Primate Center and the chimpanzee (*Pan troglodytes*) colony at the Yerkes Regional Primate Research Center, although in the predicted direction, were quite small. However, when the five colonies with less than 10% difference between inbred and noninbred infant mortality were excluded (i.e., *Galago crassicaudatus crassicaudatus*, *Saimiri sciureus*, *Macaca nemestrina*, *Macaca fascicularis*, and *Pan troglodytes*), each of the remaining 11 colonies exhibited higher inbred than noninbred infant mortality, and the trend was still significant ($P = 0.0005$, one-tailed sign test).

DISCUSSION

Inbreeding causes an increase in homozygous genotypes which, together with the general tendency for deleterious alleles to be recessive and the occurrence of overdominance at some loci, provides the genetic basis of the deleterious effects (Falconer, 1960). Many of the adverse effects of inbreeding may be due to several pairs of recessive alleles affecting the same trait. Although each pair of alleles may have only a slightly deleterious effect, their combined effects produce an animal which is usually less able

to cope with its environment than a less inbred animal. Genetic factors are known to influence susceptibility to many infectious and noninfectious diseases in both domestic animals (Lasley, 1978) and humans (Cavalli-Sforza and Bodmer, 1971). It is usually not the disease itself which is inherited but a weakness in the body which increases the probability that the disease will appear. Many examples are cited by Cavalli-Sforza and Bodmer (1971), who also illustrate the way in which inbreeding can increase susceptibility to disease (threshold model of disease).

The degree of prereproductive mortality should theoretically increase with the degree of inbreeding, and this effect has been substantiated in humans (Cavalli-Sforza and Bodmer, 1971). Our sample sizes were too small and too unevenly distributed with respect to the degree of inbreeding to enable us to expect to be able to detect any correlation between these variables within the individual colonies. We considered the possibility of combining the data across colonies and then testing for this effect, but decided against such an approach because (1) inbreeding coefficients of the same magnitude in different colonies do not indicate that the same number of pairs of alleles has become identical by descent but only that the percentage increase was identical (Falconer, 1960); and (2) a given degree of inbreeding would not necessarily be expected to have the same effect in different species because species that naturally inbreed in the wild to some extent should be less affected when inbred in captivity.

In some of the species of nonhuman primates we surveyed, the magnitude of the effect of inbreeding on infant mortality appears to be considerably greater than that reported in humans. There are several possible explanations for an extremely high rate of infant mortality in the inbred young: (1) some species may have a higher "genetic load" than humans; (2) the founding animals of some colonies may, by chance, have possessed an unusually large number of deleterious recessive alleles; and (3) the effect of a given degree of inbreeding may become proportionally greater as environmental conditions become more stressful. In some instances, noninbred young may have had an unusually low mortality rate because of some special circumstance. For example, all eight noninbred young in the mandrill data were born to a single female that was the dominant female in the group. However, possible effects of dominance status across the colonies as a whole could be excluded since several of the colonies in which animals were maintained as pairs of family groups (in which both inbred and noninbred young were born either to the dominant or to the only female in the enclosure) still showed considerably higher infant mortality in the inbred young than the noninbred young.

We have not analyzed the data with respect to the many other variables that might influence infant mortality, such as population density,

birth season, management changes, birth order of the young, and possible differences between captive-born and wild-caught females; many of these data were not available. However, detailed analyses of similar data on 12 ungulate species, in which 11 of the 12 showed a higher juvenile mortality rate in inbred than in noninbred young, demonstrated that none of these factors could account for the higher mortality rate of the inbred young (Ralls *et al.*, 1980; Ballou and Ralls, 1982). Although these findings cannot automatically be generalized to primates, inbreeding has repeatedly been shown to result in increased juvenile mortality in laboratory (Wright, 1977; Festing, 1979), domestic (Lasley, 1978), and zoo mammals belonging to several orders (Ralls *et al.*, 1979; Ralls and Ballou, 1982), as well as in humans (Cavalli-Sforza and Bodmer, 1971), and such taxonomically distant organisms as insects and plants (Wright, 1977; Frankel and Soulé, 1981), and there is no theoretical reason to expect nonhuman primates to differ from other mammals in this respect.

Even if the number of founding individuals and degree of inbreeding were constant across colonies, which they were not, it would be impossible to determine whether the variation we found in the size of the difference between inbred and noninbred infant mortality rates, and the exception to this trend in the pig-tailed macaque, represent species differences or chance effects due to choice of founding individuals. Repeated studies with laboratory and domestic animals have shown that the results of any particular inbreeding experiment with a given species may not be typical of the usual results of inbreeding in that species. For example, Bowman and Falconer (1960) found that 19 of 20 colonies of laboratory mice maintained by exclusive sibling mating became extinct by generation 12 because of the deleterious effects of inbreeding but that the remaining colony showed no decline in litter size and became a successful inbred line. Lasley (1978) summarizes similar data on dairy cows and other domestic animals.

Theoretically, species that naturally inbreed in the wild to some degree should show less of a deleterious effect when subjected to inbreeding in captivity. Not much is known about the extent to which most primate species inbreed in the wild. Smith (1979) and Bengtsson (1978) pointed out that father-daughter mating should occur in polygynous species if the advantages of having a greater proportion of one's genes represented in one's offspring are greater than the cost due to inbreeding. The best data available are for several species of macaques and baboons; these indicate that close inbreeding is rare. In many species all or nearly all young males leave their natal troop before breeding, with the result that there are few opportunities for matings between close relatives (Dittus, 1979; Wade, 1979; Greenwood, 1980). In chimpanzees (Pusey, 1980) and gorillas (Harcourt, 1978) it is females that tend to leave their natal troop; in

monogamous species, juveniles of both sexes disperse (Greenwood, 1980). Natal dispersion of both sexes has also been observed in hamadryas and gelada baboons (Kummer, 1968; Dunbar and Dunbar, 1975), purple-faced langurs (Rudran, 1973), mantled howlers (Jones, 1980), red colobus (Marsh, 1979), and white sifaka (A. Jolly, personal communication).

It has been suggested by several authors that the avoidance of inbreeding is an important function of single-sex dispersal in primates and other taxa (Clutton-Brock and Harvey, 1976; Wade, 1979; Greenwood, 1980). Packer (1979) showed that dispersing *Papio anubis* males transferred to troops with both fewer and more potentially fertile females than in their natal troops, suggesting that this behavior cannot be interpreted solely as a means for the males to increase the number of females available to them.

Wade (1979) summarized field data on migration rates between troops and estimated the genetic consequences. He concluded that the level of inbreeding in nonhuman primates is largely a consequence of the rate of migration by individuals, usually only of one sex, between social units and that many primate species live in relatively outbred troops. The bonnet macaque (*Macaca radiata*) may be an exception: both Wade and Rauf Ali (unpublished data) suspect that this species may inbreed in the wild to a considerable extent. However, levels of heterozygosity in this species have been shown to be comparable to those of other macaque species (Nozawa *et al.*, 1977). Tilson (1981) observed a mother-son mating in gibbons after the death of the father but suggested that such an event occurred relatively rarely. Sade (1968) and Missakian (1973) quantified copulation frequencies between relatives in the same provisioned population of rhesus macaques. Sade found that only 1.1% of the total copulations occurred between mother-son pairs; Missakian reported 5.4%.

Behavioral avoidance of mating between close relatives has been described by Packer (1979) in baboons, *Papio anubis*, and Pusey (1980) in chimpanzees. Packer found that juvenile female baboons stayed closer to males that were present in the troop when they were born than to males that subsequently joined it; however, once the females began to show estrous cycles, they consorted less with these familiar males. One female actively avoided overtures of a male thought to be her father. Pusey found that female chimpanzees' associations with their previous closest male associates, who were usually maternal siblings, dropped sharply when the females began to show full estrous cycles. Sexual activity was very infrequent between maternal siblings and between mothers and sons. Transfers of females to new groups seemed to result from attraction to unfamiliar males and Harcourt (1978) argues that many animals seem to prefer unfamiliar mates. He believes this preference is a common cause of emigration.

Wilson *et al.* (1975) believed that the apparently rapid rates of chromosomal evolution in primates and some other mammals indicate that these animals often inbreed in the wild. However, Schwartz and Armitage (1980) disagreed with this view on the basis of their data on yellow-bellied marmots, *Marmota flaviventris*, which they believe may be characteristic of many other mammalian species. Both behavioral observations and electrophoretic data indicated that marmots rarely mated with close relatives although they live in one-male groups or "harems."

Baker and Marler (1980), describing behavioral adaptations that have the effect of making many vertebrates tend to stay close to or return to their birthplace for breeding, argue that populations may be composed of relatively close kin more often than usually supposed. Baker and Marler also argue that the greater survival of noninbred captive ungulates found by Ralls *et al.* (1979) might be explained by heterosis between "differentially coadapted genomes" and that the low survival rate of the inbred young in the study might be normal. However, in 6 of 12 ungulate species subsequently analyzed in detail, inbred young still suffered from higher mortality rates than noninbred young when comparisons were made using only those offspring whose parents' origins were both temporally and spatially similar (Ballou and Ralls, 1982); furthermore, mortality rates for inbred young reached 100% in some species, which seems unlikely to represent normal mortality.

An important consideration when discussing the extent of inbreeding in both captive and noncaptive populations is that inbreeding is a relative rather than an absolute term. An individual can only be described as "inbred" with respect to some baseline population. In this study, we used the founding individuals of each colony as the baseline population and evaluated only the effects of inbreeding subsequent to the founding of the colonies. Individuals in natural populations may often be both "noninbred" compared to the offspring from parent-young or sibling matings and "inbred" with respect to the infinite, randomly mating population used in theoretical population genetics (Crow and Kimura, 1970). Although data from primate field studies suggest that the degree of proximal inbreeding is generally smaller than that in many captive colonies, there may be cumulative inbreeding due to small population size in some species (Spielman *et al.*, 1977).

We believe we have shown that inbreeding in captivity usually results in higher juvenile mortality in a wide variety of exotic species (Ralls *et al.*, 1979, 1980; Ralls and Ballou, 1982; Ballou and Ralls, 1982). The data presented in this paper indicate that inbreeding in captive primate colonies also generally results in increased levels of infant mortality, regardless of the extent to which primates in breed in the wild. We concur with the

suggestion of Smith (1980) that colony management practices be modified, wherever possible, to reduce inbreeding levels.

ACKNOWLEDGMENTS

We thank John Senner and Richard Van Horn for the data from the Oregon Regional Primate Research Center; Thomas Clarkson, Noel Lehner, and Francis Lusso for the data from the Bowman Gray School of Medicine; James Ogden for the data from Rush Presbyterian St. Luke's Medical Center; Devra Kleiman and Ronald Evans for the data from the 1979 Golden Lion Tamarin Studbook; Gene Sackett for the data from the Seattle Regional Primate Research Center; Pradhat Sehgal and Kathleen Grant for the data from the New England Regional Primate Research Center; Martin Curie-Cohen for the data from the Wisconsin Regional Primate Research Center; William Conway and Dan Wharton for the data from the New York Zoological Park; Frederick King and Susan Cone for the data from the Yerkes Regional Primate Research Center; Gisela Epple and Mary Scott-Cebul for the data from the Monell Chemical Senses Center; Richard W. Thorington, Jr., and Nancy Muckenhirn for advice on primate breeding centers; William Conway, Devra Kleiman, James V. Neel, Alison Jolly, Craig Packer, and Miles Roberts for helpful comments on early drafts of the manuscript; Lee-Ann Hayek for statistical advice; and Ken McCormick, Janet Alverson, and Margaret Welke for help in processing the data.

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