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Maternal Age, Parity, and Reproductive Outcome in Captive Chimpanzees (*Pan troglodytes*)

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Abstract

As early as the 1970s, it was suggested that nonhuman primates may serve as models of human reproductive senescence. In the present study, the reproductive outcomes of 1,255 pregnancies in captive chimpanzees (*Pan troglodytes*) were examined in relation to parity and its covariate, maternal age. The results show that the percentage of positive pregnancy outcomes was negatively correlated with increasing parity. In addition, spontaneous abortions, stillbirths, and caesarian sections (C-sections) were positively correlated with increasing parity. Maternal age, rather than parity, was found to be the most important predictor of negative birth outcome. This study supports research demonstrating reproductive decline and termination in nonhuman primates, and is the first to quantitatively account for this phenomenon in captive female chimpanzees.

Keywords

chimpanzee; reproduction; menopause; fetus; parity; maternal age

INTRODUCTION

Understanding the reproductive lifespan of nonhuman primates is important for captive breeding programs and the formulation of comparative concepts of senescence and birth risk. In particular, there have been numerous theoretical discussions among anthropologists, biologists, and primatologists about the presence of menopause throughout human evolution (see Alvarez [2000] for review). Lifespans predicted from body and brain size in early *Homo* suggest that a female post-reproductive interval predates *Homo sapiens* [Judge & Carey, 2000]. Today, 99.1% of human females experience a post-reproductive interval that lasts, on average, 29 years [Caro et al., 1995]. Thus, the question of whether other mammals, particularly nonhuman primates, experience menopause or a substantial post-reproductive period of life remains a central topic of discussion.

In one comparative study of 13 captive primate species, Caro et al. [1995] reported that 60% of chimpanzees, 47% of golden lion tamarins, 45% of lemurs, 40% of gorillas, 32% of squirrel monkeys, 32% of orangutans, 26% of pigtail macaques, 20% of saddleback tamarins, and 13%

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of rhesus macaques showed evidence of reproductive termination prior to death. More recently, Nishida et al. [2003] found that 25% of wild female chimpanzees at Mahale experienced a post-reproductive interval from last parturition (LP) to death (D) (minus 5 years, to account for maternal investment in final offspring (LP-D-5)). Given the high proportion of nonhuman primates undergoing significant declines in reproductive functioning, it is difficult to deem menopause the result of selective forces that act uniquely on humans (see Peccei [2001] for review). Even the earliest literature offered strong arguments that various nonhuman primates, particularly chimpanzees, can function as models of the human climacteric and the reproductive life cycle [Gould et al., 1981; Graham, 1979].

Nevertheless, Pavelka and Fedigan [1999] raised important considerations regarding reproductive termination research in nonhuman primates, including 1) the small number of mature females with sufficiently documented reproductive histories, 2) the absence of criteria for defining “menopause” in nonhuman primates, and 3) the difficulty of making cross-species comparisons, because reproductive history is environmentally dependent and varies widely across populations. With respect to chimpanzees, Bellino and Wise [2003] also noted the limited number of mature females available for research, and suggested that they appear to be a poor model of the human menopausal experience. Bellino and Wise [2003] asserted that reproductive cycles in chimpanzees continue until the end of their lives, or terminate within the last year of life, and that conception rates are the only indication of reproductive decline. However, these assertions are inconsistent with data reported by Nishida et al. [2003]. Similarly, Gould et al. [1981; p. 165] stated that “there is now no question that individuals of the genus *Pan* can attain menopause, but the age of onset may be idiosyncratic, as among women. As menopause (especially peri-menopausal changes over a protracted period) becomes more fully documented in chimpanzees, chimpanzees may become a more attractive model for the study of human reproductive senescence.”

Rather than focusing on reproductive cycling as the only indicator of reproductive cessation, we chose to follow recent studies suggesting that other measures, such as birth outcome, birth weight, and interbirth interval (IBI), may also be indicators of reproductive decline. For example, in pigtailed macaques (*Macaca nemestrina*), Ha et al. [2000] found that birth weight increases with increasing parity and decreases with the age of the dam. Similarly, in another study the birth weights of Djungarian hamster pups were positively correlated with increasing maternal age [Edwards et al., 1998]. Ha et al. [2000] cited inconsistencies in the literature as to whether IBI increased and fecundity decreased with maternal age, but they showed in analyses of 2,040 pregnancies that IBI increased linearly with parity by .27 months per pregnancy [for parities (1–7) $M = 15.2$ mo; (8–11) $M = 17.1$]. Comparative work by Caro et al. [1995] showed that IBIs for common marmosets, squirrel monkeys, macaques, apes, and humans lengthened with dam age. Finally, although they found no significant IBI correlation with maternal age, Nishida et al. [2003] reported interesting sex differences in IBI, with an average IBI of 72 and 66 months for male and female offspring, respectively. Regarding measures of reproductive outcome, one trend in the literature suggested that the probability of a viable outcome significantly decreased with increasing maternal age and parity [Dahl, 1999; Gadow et al., 1991; Ha et al., 2000]. At the same time, other work in humans suggested that primiparous mothers are at high risk for complications and nonviable outcomes [Bai et al., 2002; Dasgupta et al., 1997; Ingemarsson & Källén, 1997]. In one study of 8,488 pregnancies, more than half (53.6%) of the perinatal deaths occurred in primiparous women [Dasgupta et al., 1997]. In contrast, research by Anderson et al. [2000] showed an effect of increased spontaneous abortion, ectopic pregnancy, and stillbirth with increasing age in 634,272 Danish women that was independent of parity, number of previous spontaneous abortions, or calendar period. Particularly robust in this study were data that showed that the risk of spontaneous abortion ($n = 101, 339$) increased from 9% in 20–24-year-old women to 75% in women above 45 years of age.

To our knowledge, there is no longitudinal, empirical documentation of reproductive outcome in relation to maternal age and parity in chimpanzees. The reproductive and hormonal profiles of female chimpanzees are not entirely different from those of humans [Dahl, 1999]. Thus, they may serve as a good model for assessing reproductive outcome in relation to female characteristics, including age and parity. The purpose of this study was to evaluate whether increased parity and maternal age have a negative effect on reproductive outcome in chimpanzees. Although we did not directly assess whether female chimpanzees experience menopause, we were interested in determining whether increasing maternal age or parity had a negative consequence on pregnancy outcome. We hypothesized that if female chimpanzees do not experience reproductive termination, and can effectively breed until they die without consequences for the fetus, there should be no significant association between reproductive outcome, and maternal age, and parity.

MATERIALS AND METHODS

Subject Demographics and Data Collection Procedure

The birth records of 272 female chimpanzees with 1,255 documented pregnancies were compiled from computerized animal record systems at the Yerkes National Primate Research Center (YNPRC; Atlanta, GA), The University of Texas M. D. Anderson Cancer Center (UTMDACC; Bastrop, TX), and the Alamogordo Primate Facility (APF; Alamogordo, NM). Analysis of the animal records yielded data for each pregnancy that included dam age at parturition ($n = 1,253$), parity of the pregnancy ($n = 1,255$), gestation length ($n = 514$), IBI ($n = 1,032$; mother-raised $n = 73$; human-raised $n = 166$), sex of offspring ($n = 1,123$), birth weight ($n = 673$), and parturition type (spontaneous abortion/miscarriage ($n = 162$), stillbirth ($n = 99$), caesarian section (C-section; $n = 50$), or live vaginal delivery ($n = 944$)). Based on the parturition type information, reproductive outcome was a dichotomous variable that was classified as positive when parturition was a live vaginal birth, and negative when parturition was 1) a spontaneous abortion signifying a natural termination of the pregnancy and expulsion of pregnancy tissues/fluids, 2) a stillbirth signifying the delivery of a nonviable fetus, or 3) a C-section signifying a surgically assisted delivery.

Birth weights were measured in kilograms, and it is unknown whether the birth weights were taken dry or wet. Gestation length and maternal age were measured in days and years, respectively. Sex of offspring was determined postpartum, if possible. We did not include data regarding birth weight, gestation length, or sex of offspring in the analyses for this study [Fessler et al., 2005]. The IBI was calculated as the interval from the date of one parturition to the next. All confirmed pregnancies within an individual chimpanzee's lifespan, independent of outcome, were included in the determination of parity. No restrictions were made for twinning or non sequitur parities. However, information from pregnancies that lacked parity data points was excluded from the analyses.

RESULTS

Descriptive Statistics

For our initial data set, the average dam age at parturition was 18.6 years ($SD=6.6$), average parity was 4.9 ($SD = 3.5$), and average IBI was 2.1 years ($SD=1.4$). The average IBI for mothers that raised their infants was 2.8 years ($SD=1.57$), and the average IBI for mothers that did not raise their infants was 2.1 years ($SD=1.55$). The average gestation length was 217.3 days ($SD=39.1$). There were 560 females, 563 males, and 132 unknowns. In terms of parity, 216 pregnancies were primiparous, 470 were parities of 2–4, 305 were parities of 5–7, and 264 were parities of 8 or more. Initially, because parity and maternal age were significantly positively correlated ($r = .798$, $df = 1,253$, $P < .001$), we used only one variable, parity, in

subsequent analyses. For these analyses, we classified the subjects into eight different categories of parities (1st, 2nd, 3rd, 4th, 5th, 6th, 7th, and 8th +). Instead of retaining the literal parities beyond 8 (where n's became low), we included in the 8th category pregnancies with parities of 8 or higher. We selected 8 as the maximum parity cutoff point because the average number of pregnancies in our sample was 4.86, with an SD of 3.46. Therefore, pregnancies with parities of 8 or higher constituted those that were more than 1 SD above the average parity.

Effects of Parity on Reproductive Outcome and Fetal Mortality

In our initial data analysis, we performed a chi-square test of independence to examine the interaction between parity and reproductive outcome (positive or negative). A chi-square test of independence revealed a significant influence of parity on reproductive outcome: $\chi^2 (8, n = 1,255) = 45.70, P < .05$. Table I shows the percentages of positive ($n = 976$) and negative ($n = 279$) pregnancy outcomes as a function of parity. As expected, the percentage of positive outcomes decreased with increasing parity. Indeed, for pregnancies with parities of 8 or higher, more than 35% of the pregnancies had a negative outcome in contrast to pregnancies with lower parities (range=13–26%).

To further explore the relationship between parity and reproductive outcome, we performed a second chi-square test of independence on the specific parturition type. For this analysis, we used a series of chi-square tests of independence to compare the distribution of live births to stillbirths, spontaneous abortions, and C-sections across parities. Significant differences in distributions were found between live births and spontaneous abortions ($\chi^2 (7, n = 1,106) = 39.079, P < .001$) and stillbirths ($\chi^2 (7, n = 1,043) = 20.551, P < .01$), but not between live births and C-sections ($\chi^2 (7, n = 994) = 12.322, P > .05$). The percentages of spontaneous abortions, stillbirths, and C-sections are shown in Figure 1. These results indicate that the risk of aborting the fetus or having a stillbirth increased with increasing parity. However, the risk of having a C-section did not change with parity.

In the previous analyses, all pregnancies were considered independent events. However, this was not entirely the case, since females contributed different numbers of data points to the analysis. A better way to evaluate reproductive outcome as a function of parity (and maternal age) is to perform longitudinal analyses of reproductive outcome throughout the lifespan of the same individuals. These data were available for 73 females from our sample. For each female, we calculated the percentage of live offspring born at parities ranging from 2–4, 5–7, and 8 or higher. These percentages were compared by means of a one-way repeated-measures analysis of variance (ANOVA). The ANOVA revealed a significant main effect for parity ($F (2, 144) = 13.56, P < .05$). A subsequent post-hoc test using the least-squared difference showed that the percentage of live offspring was significantly higher in parities of 2–4 (84%) and 5–7 (82%) compared to parities of 8 or higher (63%). The results largely confirm the chi-square results.

Predictor of Negative Reproductive Outcome: Maternal Age or Parity?

In the previous analyses, we focused solely on the influence of parity on reproductive outcome. However, it was of theoretical interest to know which variable—maternal age or parity—accounted for the most variability in reproductive outcome. Multiple regression analyses seemed appropriate for this question, but because parity and maternal age were so strongly correlated, there was a problem of collinearity among predictor variables. To address this issue, we approached the question differently by performing a series of ANOVAs and analyses of covariance (ANCOVAs). Initially, we ran two ANOVAs with parity and maternal age serving as the dependent variables and reproductive outcome serving as the independent variable. We subsequently ran two ANCOVAs with either maternal age or parity serving as the dependent variable and the correlated subject variable serving as the covariate. Reproductive outcome

remained the independent variable. Not surprisingly, significant differences in maternal age ($F(3, 1249)=19.37, P<.001$) and parity ($F(3, 1251)=11.59, P<.001$) were found as a function of reproductive outcome. However, the ANCOVA results revealed that maternal age remained significantly different as a function of reproductive outcome when parity served as the covariate ($F(3, 1248)=4.88, P<.01$). The average maternal ages for spontaneous abortions, stillbirths, and C-sections were significantly higher than for live vaginal births. The opposite condition was not true and parity differences were no longer significantly different when maternal age served as the covariate. Thus, these analyses suggest that increasing maternal age is the most important variable contributing to variability in reproductive outcome.

Interbirth Interval

The average IBI was 2.09 years for multiparous pregnancies. No significant difference in IBI was found as a function of reproductive outcome in the sample. Thus, IBI was unrelated to reproductive outcome. Maternal age was positively correlated with IBI ($r=.228, df=1030, P<.01$) indicating that older females had longer IBIs. Even after the subjects were separated by rearing history, maternal age and IBI for mother-raised and human-raised infants were still positively correlated ($r=.313, df=71, P<.01$; $r=.156, df=164, P<.05$).

DISCUSSION

The results of this study are relatively straightforward. Increasing parity and maternal age have significant consequences for reproductive outcome. In particular, there are increased risks for spontaneous abortions and stillbirths associated with increasing age and parity. These results were evident in both cross-sectional and longitudinal analyses on reproductive outcome. To determine whether parity or maternal age is the most relevant variable in predicting reproductive outcome, we performed additional analyses, which indicated that maternal age is the most important variable.

Comparable findings in other species vary with regard to the influence of maternal age and parity on reproductive outcome. Bales et al. [2001] found no evidence of an age-related reduction in fertility in wild golden-lion tamarins (*Leontopithecus rosalia*). In a population of ring-tailed lemurs (*Lemur catta*), Gould et al. [2003] found the greatest amount of variability in fecundity in a cohort of older females. Ha et al. [1999] showed that the probability of a viable outcome decreased from 93% with the first pregnancy to 85% with the sixth pregnancy in a population of captive pigtailed macaques (*Macaca nemestrina*) (also see Westergaard et al. [2000]). In comparison with the macaque data presented by Ha et al. [1999], the proportion of viable outcomes is much lower in chimpanzees for high parity pregnancies; however, it is difficult to compare rates because of the various life histories of the different primate species.

There were also some differences in our findings in comparison with data on reproductive outcome and life history in wild chimpanzees. Our sample of captive chimpanzees had a shorter IBI, higher number of live offspring, and lower maternal age at first parturition than were found among wild chimpanzees in Gombe and Mahale [Goodall, 1986; Nishida et al., 2003] (see Table II for a comparison between our results and those from Mahale). The disparity between these numbers is attributed to the inclusion of captive females that produced large numbers of offspring, and particularly those that exhibited inadequate maternal care. Inadequate mothers did not take care of their offspring, and therefore the infants were raised by humans in a nursery setting [Bard, 1996]. In the absence of lactational amenorrhea, these females began to cycle and conceive more quickly relative to wild chimpanzees, which caused reduced IBIs and subsequently more offspring.

This causes problems of interpretation with respect to the natural course of reproductive outcome, maternal age, and parity because it does not necessarily approximate normal

reproductive processes in wild chimpanzees. However, one could argue that the breeding practices used at these facilities “stressed” the reproductive system of the chimpanzees to its maximum capacity, and allowed, in essence, a threshold for the breakdown of their system (which is more difficult to evaluate in wild chimpanzees) to be determined. Also, the sources of mortality in captive chimpanzees are reduced compared to those in wild populations, since predation and poaching are not causes of death in captivity. Moreover, exposure to natural elements, parasitic load, disease, and infant death due to abandonment or maternal death are significantly decreased owing to better nutrition, veterinary care, and shelter. Therefore, our sample allowed for a more complete reproductive history to be obtained from a larger sample of females than would typically be available in wild apes.

Here, maternal age, as opposed to parity, was shown to be the most important predictor of negative birth outcome in chimpanzees. This supports well-established research in women, which indicates that viability decreases and negative birth outcomes (e.g., Down's syndrome, birth defects, and spontaneous abortions) increase with maternal age (see Newburger [2000] for review). In fact, studies indicate that the chance that a woman over 40 years of age can have a successful pregnancy is poor [Anderson et al., 2000; Fretts et al., 1995]. Collectively, these data suggest that reproductive outcome is compromised with increasing maternal age in human and nonhuman primates. In short, although the extent of the post-reproductive interval in nonhuman primates remains unclear, they do experience cessation in reproduction, albeit at different rates and possibly due to different mechanisms.

In conclusion, our results indicate a significant influence of maternal age and parity on reproductive outcome in captive chimpanzees. The mechanisms responsible for this pattern of results remain unclear. One interpretation is that the decline in fetal viability is due to hormonal changes, not unlike those known to occur in women and other nonhuman primates [see Bellino et al., 2003; Gould et al., 1981; Walker, 1995]. Unfortunately, hormone data from pregnant female chimpanzees are virtually absent, and we have none from pregnant older females who experienced different reproductive outcomes [Dahl, 1999]. Alternatively, reductions in fetal viability may result from a breakdown in peripheral reproductive organs due to age or increased parity, which simply cannot sustain repeated pregnancies. Previous studies in macaques reported that social factors during pregnancy contribute to reproductive outcome [Boot et al., 1985; Ha et al., 1999; Westergaard et al., 2000]; however, this variable was not considered in the present study. Additional research, particularly in elderly apes, is clearly needed. Lastly, an area of research that seems to be overlooked despite its considerable relevance to this topic, is the consequences for the fetus developing in an aged female primate. Assuming that the prenatal environment of the developing fetus in an older female is relatively unstable, it might be predicted that offspring born to older females may be compromised in some specific behavioral, physiological, or cognitive manner that reduces their individual fitness compared to offspring born to younger females. Addressing this question would offer yet another alternative approach for evaluating the advantages and disadvantages of reproductive cessation in primates, including humans.

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Fig 1.
Percentage of stillbirths, spontaneous abortions, and C-sections as a function of parity.

TABLE I

Positive and Negative Reproductive Outcomes Across Parity

Parity	Negative (%)	No.	Positive (%)	No.	Total no.
1	19.90	43	80.10	173	216
2	12.60	23	87.40	159	182
3	13.70	21	86.30	132	153
4	21.50	29	78.50	106	135
5	22.70	27	77.30	92	119
6	25.70	26	74.30	75	101
7	18.80	16	81.20	69	85
8+	34.94	94	64.39	170	264
Total	22.20	279	77.80	976	1,255

TABLE II
Comparison of Means Between Subjects and the Wild Chimpanzee Population of Mahale

Measure	Current captive sample	Mahale wild population ^a
Interbirth interval (mo)	25.18	69.06
No. of live offspring	4.49	3.39
Maternal age at first parturition (yr)	11.66, n = 214	15.6, n = 5 (in natal group) 14.65, n = 26 (in transfer group)

^aThe wild chimpanzee population of Gombe had comparable means to Mahale.