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RESEARCH ARTICLE

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Stillbirth rates across three ape species in accredited American zoos

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Stillbirths, or births of infants that died in the womb, represent a failure of the materno-feto-placental unit to maintain a suitable fetal environment. Typical studies of nonhuman primate (NHP) stillbirth patterns are primarily descriptive and focus on macaques (genus *Macaca*). Thus, less is known about other NHP species and rarer still are studies that examine possible biological factors that influence stillbirth rates across taxa. To examine possible contributors to stillbirths in great apes, we analyzed 36 years (1980–2016) of historical data documenting births of zoo-housed chimpanzees (*Pan troglodytes*, $N = 391$), western lowland gorillas (*Gorilla gorilla gorilla*, $N = 491$), and orangutans (*Pongo spp*, $N = 307$) in accredited zoological parks in the United States. The average number of births for each of the 446 mothers was 2.7, resulting in a total of 1,189 births with 143 stillbirths (12%). Stillbirths represented 12% of chimpanzee births, 13% of gorilla births, and 10% of orangutan births. We used generalized linear mixed-effects models to assess possible relationships between stillbirth likelihood and mother origin (wild- versus captive-born), age, and genus. Across taxa, older mothers were more likely to have a stillbirth ($p = 0.004$). While these results are likely influenced by both biological and management-related factors (e.g., selective captive breeding), they may be useful to population managers in evaluating pregnancy risks for great apes. Captive settings and archival studbook data such as these may provide a unique opportunity to further explore this topic.

KEYWORDS
captive, pregnancy, primate, zoo management

1 | INTRODUCTION

Stillbirths, which occur when the materno-feto-placental unit fails to maintain a suitable fetal environment, can be defined as the birth of fetuses that died in the womb (Sesbuppha et al., 2008). The underlying causes of stillbirths are not well understood or documented, though many potential causes, such as stress, have been studied. Though stillbirths may be relatively common for all placental mammals, much of what is known about them comes from studies of humans. In humans, stillbirth rates, which average around 2% worldwide (Lawn et al., 2011), increase with maternal age (Reddy, Ko, & Willinger, 2006) and poor nutrition (Ngoc et al., 2006). Other factors such as psychological stress, socioeconomic status, and race also influence human stillbirth rates (Ngoc et al., 2006; Silver et al., 2007; Wisborg, Barklin, Hedegaard, & Henriksen, 2008).

A comprehensive study conducted by the The Lancet (Lawn et al., 2011) found that only 2% of worldwide stillbirths occur in high income countries, suggesting that access to healthcare and socioeconomic status are important predictors for stillbirth likelihood in humans. Most interventions, however, focus primarily on survival after birth for human infants, leaving efforts to decrease stillbirths behind. As such, few biological studies have investigated underlying causes of stillbirth likelihood (Lawn et al., 2011). Silver et al. (2007) note obstetric conditions and disease as the highest contributors of fetal death. Many stillbirths are still characterized as having an undetermined cause, a result that often is attributed to lack of data (Lawn et al., 2009).

In order to better understand the underlying causes of stillbirths, researchers have turned to nonhuman primates (hereafter NHPs) (Sesbuppha et al., 2008). Stillbirths are relatively common in NHPs, but causes are as varied and unknown as those for humans. Sesbuppha et al. (2008) studied stillbirths in long-tailed macaques (*Macaca fascicularis*) over a 7-year period, noting causes such as trauma, fetal pneumonia, and uterine rupture. Frias et al. (2011) studying Japanese macaques (*Macaca fuscata*), discovered that high-fat food consumption led to inflammation of and reduced blood flow to the uterus, resulting in stillbirths. In a study of pregnancies (N = 1,255) of captive chimpanzee mothers, Roof et al. (2005) found that maternal age was an important predictor of stillbirth incidence. While these studies have helped form the foundation of our understanding of NHP stillbirth patterns, there is a dearth of comparative evaluations in which multiple phylogenetically-related species are examined using similar methods. Such approaches hold the potential to not only inform our understanding of stillbirth incidence in placental mammals, but also to aid population management programs for captive animals (Roof, Hopkins, Izard, Hook, & Schapiro, 2005). Management programs consider several factors, including demography and relatedness to others, before making breeding recommendations for captive animals (Long, Dorsey, & Boyle, 2011) and individuals are not given equal opportunity to breed because of this. Therefore, more information on the factors influencing stillbirths in individuals will be useful to the successful management of NHPs, especially those populations that are threatened in the wild.

Using archival studbook data, the current project explored possible relationships between stillbirth rates and origin, age, and genus in three zoo-housed ape taxa: chimpanzees (*Pan troglodytes*), western lowland gorillas (*Gorilla gorilla gorilla*), and orangutans (*Pongo spp*). Relatively little is known about stillbirths in these genera, as NHP stillbirth studies are often based on macaques and are primarily descriptive. As each has varied reproductive cycles, we hypothesized that we would find taxonomic differences in the influences and rates of stillbirths. We also hypothesized that age would be a significant predictor of stillbirth likelihood across genera based on previous studies. Accredited zoos maintain detailed records on animals they manage, providing a unique opportunity to study this poorly understood phenomenon. With this knowledge, population managers may be better prepared to lessen stillbirth likelihood and better understand factors that affect population management, genetics, and demography.

2 | METHODS

This study was approved by the Lincoln Park Zoo Research Committee, the governing body for all animal research at the institution. This research adhered to legal requirements in the United States of America and to the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates.

All data were extracted from official studbooks maintained to document the managed populations among accredited zoos. In the case of chimpanzees and gorillas, data were drawn from the North American Regional Studbooks for zoos accredited by the Association of Zoos and Aquariums (AZA). For orangutans, data were drawn from the International Studbook, as a regional studbook does not exist for orangutans. For the purposes of our analysis, only individuals living in the AZA-accredited zoo population were included.

We used data from each taxon documenting all births (still and live) from 1980 to 2016 (2014 for orangutans). We did not use data prior to 1980, as studbook record keeping became more consistent across zoos at this time. In order to maintain consistency in sample sizes across taxa, we chose to omit bonobo data, which is less abundant than the other three great ape taxa. This provided records of a total of 1189 birth events: 491 for gorillas, 391 for chimpanzees, and 307 for orangutans. The following information was available from the studbook for each individual: birth date, sex, zoo of birth, death date (if applicable), mother's identification number, the age of the mother at birth, and whether the mother was born in the wild or captivity. For the purposes of this analysis, we considered an individual to be stillborn when their date of birth and date of death were the same, as this is the standard practice for entering stillbirths in studbooks. Infants that died within a day of birth would also be captured by this practice but presumably represent a small minority. Ages for wild-born individuals were estimated based on standard studbook practices.

We used generalized linear mixed models with binomial errors to determine if mother's age, origin, or genus were correlated to the likelihood of a stillbirth event (Gelman & Hill, 2009). To do so, stillbirth events were coded as a "1" within these data while all other births were coded as a "0." Furthermore, we centered the mother age covariate before analysis. We fit seven models to these data, which included all combinations of our three predictor variables (i.e., mother age, mother origin, and genus) and one final model that only included the intercept. A mother's identification number was treated as a random effect in each model because some mothers had multiple births; therefore, not all births were independent events. This non-independence was the primary motivation for using a mixed model with these data.

To determine the most parsimonious model given the data, we compared all models via Akaike's information criterion (AIC) (Burnham & Anderson, 2003). AIC is an information theoretic approach that can be used as a means of model selection. Briefly, AIC measures the relative fit of a set of models applied to the same data as a function of a models likelihood and a penalty term that increases with the number of estimated parameters within a model. Thus, AIC discourages over-fitting of the data as including additional parameters generally increases a models likelihood. While the model with the lowest AIC value has the best relative fit, we considered all models within Δ2 AIC of the top model to have substantial support (Burnham & Anderson, 2003). To address model uncertainty, we calculated model-averaged regression coefficients based on each models AIC weight (Burnham & Anderson, 2003). For regression coefficients, we considered those with a p value equal to or less than 0.05 statistically significant. All analyses were conducted using R (version 3.3.3; R Development Core Team, 2017; www.r-project.org).

3 | RESULTS

There were 183 unique gorilla mothers, 132 unique chimpanzee mothers, and 131 unique orangutan mothers (Table 1). Of the 491 gorilla births, 63 (13%) were stillbirths, 48 of 391 (12%) chimpanzee births were stillbirths, and 32 of 307 births (10%) for orangutans. The average age at birth for gorilla mothers was 17 years (range 6–41 years), 20 years for chimpanzees (range 6–63 years), and 21 years for orangutans (range 7–47 years).

Three models were considered to have substantial support (Table 2). These models included mother age, origin, and genus as independent variables, though mother age was included in each supported model. Overall, mother age was a significant predictor of stillbirth likelihood, with older mothers being more likely to give birth to stillborn offspring ($p = 0.04$; Figure 1), and no taxonomic difference was found ($p = 0.27$; Table 3). The probability of stillbirth was very low for all genera (Figure 2). Holding mother's age constant at its mean value, the probability of stillbirth across taxa was 6.41% (95%CI = 3.62–11.11%).

To better understand the increase in stillbirth likelihood with age, we compared stillbirth rates from mothers at age 10, a time when most captive apes have reached puberty, and age 35, when many captive ape mothers do not continue reproducing either biologically or behaviorally (Atsalis & Margulis, 2006; Caro et al., 1995; Gould, Flint, & Graham, 1981; Margulis, Atsalis, Bellem, & Wielebnowski, 2007). Ape mothers at age 35 are 2.79 (95%CI = 2.47–3.15) times more likely to produce a stillborn baby than at age 10.

4 | DISCUSSION

This study analyzed 36 years of studbook data to explore possible relationships amongst maternal factors and stillbirth rates in zoo-housed great apes. As hypothesized, we found that age significantly predicted stillbirth rates across genera, with older mothers more likely to experience stillbirths (Figure 1). Total births are highest between the ages of 11 and 15 years for all three species, yet stillbirths peak between the ages of 21 and 25 years (Figure 2). This is consistent with prior research on the topic that demonstrated that stillbirths increase with age in NHPs (Roof et al., 2005; Schlabritz-Loutsevitch et al., 2008), as many aspects of reproductive ability decrease (Ha, Robinette, & Sackett, 2000; Pavelka & Fedigan, 1999). Our hypothesis that we would find taxonomic differences in stillbirth likelihood was not supported, as genus was not statistically significant.

The relation between age and stillbirth rates converges well with ongoing interest in the degree to which reproductive potential changes in the later life stages of primates. The prevalence of reproductive senescence among NHPs remains in question, though there is evidence for age-specific fertility declines in both chimpanzees (Caro et al., 1995) and gorillas (Margulis et al., 2007). The primate endometrium is an important contributor to successful pregnancies, and its healthy functioning relies heavily on estrogen and progesterone in the uterus (Okulicz, 2006). High ovarian hormone levels also increase the probability of successful conception, and estrogen in particular is associated with fertility (Emery Thompson, 2005). Studies suggest reproductive senescence in NHPs involves hormonal changes,

TABLE 1 Descriptive summary of variables and births across genera

	Pan	Gorilla	Pongo
Mean mother age	20	17	21
Maximum mother age	63	41	47
Minimum mother age	6	6	7
Number of mothers	132	183	131
Mothers (captive)	80	139	100
Mothers (wild)	52	44	31
Total births	391	491	307
Stillbirths	48	63	32

TABLE 2 AIC comparisons of each tested model combination

	df	ΔAIC	Weight
Mother age	3	0.00	0.38
Mother age + genus	5	0.93	0.24
Mother age + origin	4	1.29	0.20
Mother age + origin + species	6	2.06	0.14

Models with a ΔAIC scores below 2 were considered to have substantial support.

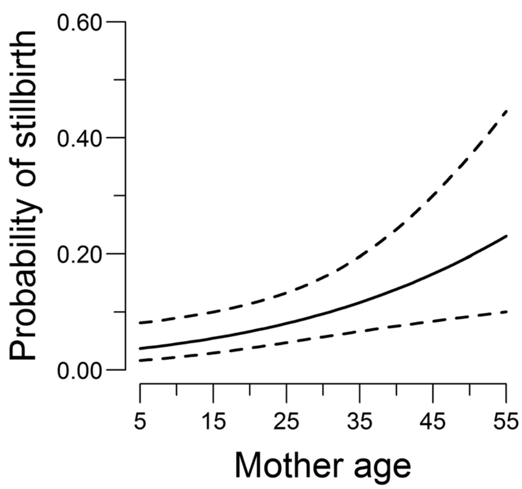

FIGURE 1 The influence that mother age has on the probability of stillbirth for all taxa. The solid line represents the predicted probability while the dotted lines represent 95% confidence intervals. Confidence intervals are based only on the uncertainty of fixed-effects within the model

TABLE 3 Model averaged regression coefficients showing relationships amongst stillbirth rate and mother age, genus, and origin

	Estimate	Std. Error	*z*-value	*p*-value
Intercept	−2.68	0.31	8.73	<2e−16*
Mother age	0.04	0.015	2.87	0.00*
Genus—*Gorilla*	0.35	0.32	1.11	0.27
Genus—*Pongo*	−0.2	0.35	0.6	0.55
Origin—captive	−0.28	0.30	0.95	0.34

*$p < 0.05$.

which, given the hormonal importance to pregnancy, likely contribute to negative pregnancy outcomes, such as stillbirths and miscarriages, later in life (Altmann, Gesquiere, Galbany, Onyango, & Alberts, 2010; Black & Lane, 2002; Wise, 2005). Issues with placental normalcy are also possible contributors to negative pregnancy outcomes as primates age (Reddy et al., 2006), though these issues may be a result of hormonal changes as well.

Though studies of wild populations indicate no evidence of NHP fertility decline with age in healthy mothers, it is important to note that the sample size of healthy, older mothers giving birth is quite low (Emery Thompson et al., 2007). Therefore, it is difficult to determine if studies on captive NHP senescence point toward a trend in captive populations only (Emery Thompson et al., 2007), or if we would see a similar trend in wild populations if life expectancy increased. Regardless, the great number of old age NHPs in captive settings provides a great opportunity to continue studying the topic of NHP senescence.

Increased parity has also been associated with increased risks of negative pregnancy outcomes, such as miscarriage and stillbirth (Ha et al., 2000; Roof et al., 2005). Parity and age, however, have been found to be significantly correlated, with age being more important in determining stillbirth likelihood than parity. Many human and nonhuman primate studies have found that, regardless of parity, age significantly predicts negative pregnancy outcomes, making maternal age at birth the more appropriate variable for this analysis (Roof et al., 2005).

Despite the breadth of this study, there are potential limitations that need be considered. We relied on the records from the official studbooks to characterize the population and the timing of birth events including stillbirths. While these records are carefully kept by trained zoo professionals, the potential for data validity issues exists and likely increases with older records. This was in part the reason we selected records only dating back to 1980, at which time formalized procedures for studbook record keeping were broadly implemented. The means by which stillbirths were recorded is also worth consideration. While the accepted form of recording keeping for a stillbirth event is to record both a birth and a death on the same day, it is possible that live births that did not survive until the second day of life were recorded in this manner and mischaracterized here as stillbirths. We expect this to be a relatively rare phenomenon and not to be recorded in a manner biased

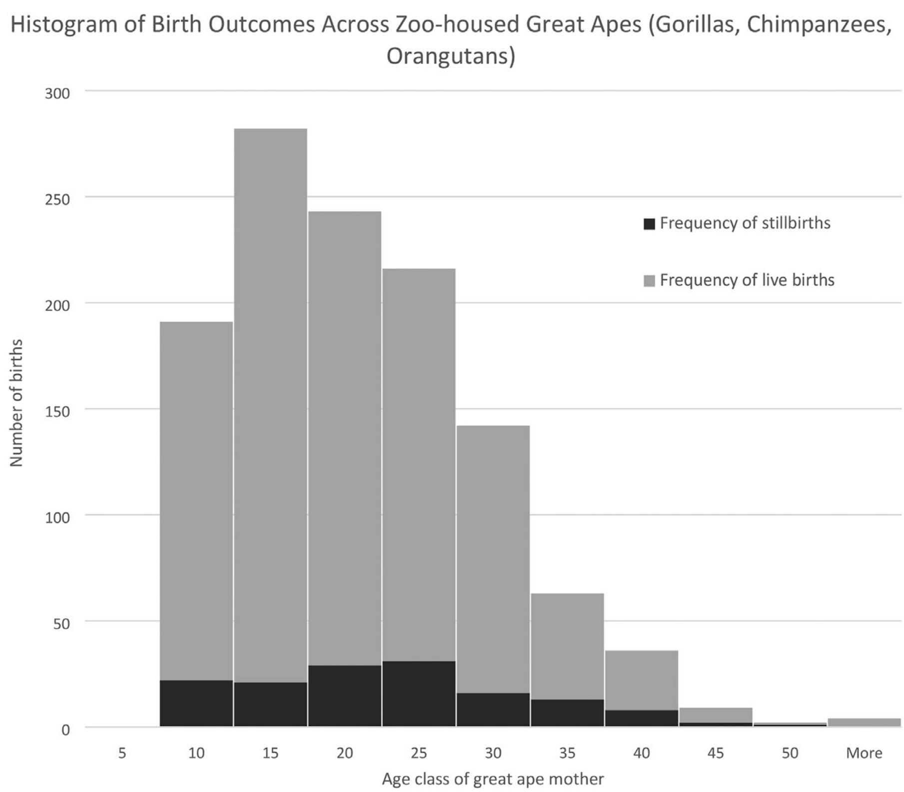

FIGURE 2 The frequency of live births and stillbirths by age class of zoo-housed great ape mother. Darker shading represents stillbirths, while lighter shading represents live births

by taxon, age, or other factors under consideration. Furthermore, some stillbirths may not have been detected or recorded at all, especially in the early records, but again we do not expect this to unduly affect our analysis. Finally, one should consider that ages of wild-born individuals are necessarily estimated and as such, subject to some scrutiny.

Overall, we found that 12% of birth events across these great ape species were stillbirths. Reports of stillbirth rates in humans seem much lower, but they vary widely across socio-economic conditions, from 0.5% in developed industrialized countries to over 3% in areas of south Asia and Africa (Stanton, Lawn, Rahman, Wilczynska-Ketende, & Hill, 2006). While these rates appear much lower than those we report for nonhuman great apes, there is growing consensus that human stillbirth rates, primarily those from developing countries, are most likely underreported (Lawn et al., 2016; McClure, Nalubamba-Phiri, & Goldenberg, 2006). Furthermore, stillbirth rates in the wild are very difficult to determine and we do not attempt here to explain any potential differences between human and nonhuman great ape stillbirth rates.

Another consideration in interpreting these findings is the degree to which these phenomena are influenced by captive management strategies. Broadly speaking, breeding decisions for these species are made as part of cooperative population management plans administered by the Population Management Center of the Association of Zoos and Aquariums through Species Survival Plan (SSP) programs. The decisions to match particular individuals for reproduction come as the result of planning that considers a number of factors including demography and relatedness to others in the population (Long et al., 2011). While population management strategies broadly aim to protect the genetic and demographic health of captive populations, species-specific strategies may vary (Leus, Traylor-Holzer, & Lacy, 2011). For instance, captive chimpanzees and gorillas in AZA-accredited zoos are generally restricted from reproducing at the age of 40 while no such cutoff currently exists for orangutans. Other strategies defining individual breeding recommendations may be less defined and may consider social group status, individual health or facility restrictions. In general, it is understood that individuals under captive management are not given equal opportunity to reproduce. We cannot discount the possibility that captive breeding decisions, based on the myriad of factors discussed above, may have some effect on stillbirth rates beyond the factors we examined.

The results of this study may help contribute to the refinement of captive breeding programs and animal management in zoological parks. From a variety of perspectives, stillbirth events represent an unwanted outcome of a population management strategy. They are viewed as risks to animal welfare and information that can assist in reducing their occurrence is needed to improve breeding management strategies. The current study helps elucidate important trends in stillbirth rates across three taxa of great apes, providing a comparative perspective on these events. We advocate for the adoption of this information to inform further refinement of captive management strategies in zoos, such as earlier cutoff ages for reproduction, and for continued use of well-administered, longitudinal records such as studbooks, to inform our understanding of birth management in other species as well.

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