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Female reproductive aging in seven primate species: Patterns and consequences

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Age-related changes in fertility have increasingly been documented in wild animal populations: In many species the youngest and oldest reproducers are disadvantaged relative to prime adults. How do these effects evolve, and what explains their diversity across species? Tackling this question requires detailed data on patterns of age-related reproductive performance in multiple animal species. Here, we compare patterns and consequences of age-related changes in female reproductive performance in seven primate populations that have been subjects of long-term continuous study for 29 to 57 y. We document evidence of age effects on fertility and on offspring performance in most, but not all, of these primate species. Specifically, females of six species showed longer interbirth intervals in the oldest age classes, youngest age classes, or both, and the oldest females also showed relatively fewer completed interbirth intervals. In addition, five species showed markedly lower survival among offspring born to the oldest mothers, and two species showed reduced survival for offspring born to both the youngest and the oldest mothers. In contrast, we found mixed evidence that maternal age affects the age at which daughters first reproduce: Only in muriquis and to some extent in chimpanzees, the only two species with female-biased dispersal, did relatively young mothers produce daughters that tended to have earlier first reproduction. Our findings demonstrate shared patterns as well as contrasts in age-related changes in female fertility across species of nonhuman primates and highlight species-specific behavior and life-history patterns as possible explanations for species-level differences.

aging | demography | maternal-effect senescence | parental-effect senescence | fertility

Significance

Age-related changes in the capability to produce healthy young are common in humans and are increasingly well documented in nonhuman animals. However, differences among species in the nature of these age-related changes remain poorly understood. We compare patterns and consequences of age-related changes in female reproductive performance in seven primate populations that have been subjects of long-term continuous study for 29 to 57 y. Our analyses of parental age effects on fertility, offspring survival, and offspring development highlight some shared patterns of parental age effects that may be general across the order primates. At the same time, we also identify species-level differences that implicate behavioral and life-history patterns as drivers of the evolution of parental age effects.

The effects of age on reproductive performance remain poorly understood in nonhuman animals, particularly in wild populations. This is true despite several decades of growth in research on age-related changes in fertility patterns in the wild (1–4), which has revealed a number of species in which either older parents or very young parents—or both—are compromised, relative to prime-aged parents, in their ability to produce healthy offspring. In wild mammals in particular, reproductive traits can often be reasonably approximated with a negative quadratic function: An initial increase in reproductive performance after sexual maturity is associated with increasing parental competence and enhanced body condition; this may then be followed by a period of prime reproductive performance and finally by a subsequent decline associated with general senescence (5–12). The effects of old versus young parental age on fertility and offspring performance are distinct, but they both have important implications for understanding the evolution of life-history traits and their correlates.

Negative effects of old age on reproductive performance—reproductive senescence—are well-known in humans and also widespread among long-lived iteroparous animals (1, 2, 13). However, the details of which reproductive traits show senescence, and in what manner, vary between species. Age-related declines in reproductive performance ("fertility senescence") and age-related reduction of offspring performance ("parental-effect senescence") represent two distinct components of reproductive senescence (14). Fertility senescence is one of the best-documented aspects of aging in wild animal populations, although data are often restricted to females (15). Evolutionary explanations for age-related declines in fertility are strongly connected to theories of biological aging, which invoke the weakening influence of natural selection with advancing age (16, 17). Parental-effect senescence, also known as the Lansing effect (18), has been well-documented in humans and in laboratory animal models (19), and more recently in a small number of wild animals (20–22). It can affect any component of offspring fitness, including offspring health, survival, rate of sexual maturation, or fecundity. For example, in humans, delayed childbearing is associated with steep increases in the risks of infant mortality, miscarriage, polysomy, and other congenital abnormalities, reduced lifespan, and other negative health outcomes in offspring

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(23–26). The mechanisms that underpin parental-effect senescence in different species remain poorly understood, but may include epigenetic influences on offspring phenotypes or age-related declines in the ability to provision and care for eggs, embryos, or dependent offspring (9, 11, 13, 27). The limited evidence on parental-effect senescence in animals thus far highlights the heterogeneity of parental-effect senescence across species, not only in which offspring traits are affected by parental senescence, but in the magnitude of the effects (3, 4).

Negative effects of very young maternal age are also frequently associated with reduced fertility and offspring performance, but as with parental-effect senescence, the effects of young maternal age on offspring performance are heterogeneous across species. For example, in Soay sheep the youngest mothers show reduced fertility, reduced offspring birth weight, and reduced offspring survival relative to prime-aged mothers (11). In contrast, in red deer, young females show reduced fertility and reduced offspring birthweight, but not reduced offspring survival relative to older mothers (28, 29). In many, but not all, nonhuman primate species, offspring of primiparous females experience higher mortality than those of multiparous females. This result has been attributed to the inexperience or relatively small body size of primiparous mothers (30–34). However, small body size and inexperience are common characteristics of primate primiparas, while a survival disadvantage for firstborn offspring is not universal, indicating that the relevance of this explanation varies across species (35).

The evolution of parental-age effects may be linked to the evolution of longevity, fertility, parental care, and social behavior (3, 4). This broad importance of parental-age effects and their implications for multiple aspects of life history and behavior highlight an important emerging question in evolutionary biology: How do these effects evolve, how do they differ between the sexes, and what explains their diversity across species? Detailed data on patterns of reproductive senescence in multiple species are required to tackle this question effectively.

In this study, we contribute data on patterns of age-related changes in fertility and age-related changes in maternal effects in wild nonhuman primates. Specifically, we compare patterns and consequences of female reproductive aging in seven primate populations that have been subjects of long-term continuous study for 29 to 57 y (36–39) (*SI Appendix*, Table S1). For example, previous studies on these populations have documented age-related changes in mortality, contributing to our understanding of the evolution of senescence (37, 40, 41), and species-specific patterns of age at last live birth, contributing to our understanding of the evolution of human menopause (38). High-quality individual-based datasets on aging in wild animals are uncommon and difficult to gather (42), making this dataset a unique and exceptionally valuable resource for examining female reproductive aging in our closest living relatives. Our cross-species approach provides a comparative landscape in which the evolution of human aging and reproduction can be situated and allows us to test for both components of reproductive senescence: fertility senescence and parental-effect senescence. First, we aimed to determine how variable are patterns of age-related changes in female fertility across primate species, focusing specifically on whether a cross-species signature of aging could be reliably detected as a lengthening of interbirth intervals (IBIs) after the birth of a surviving offspring with advancing maternal age. Second, we sought to determine whether maternal age effects could be observed in components of fitness in the next generation, focusing on offspring survival during infancy and age at first reproduction (AFR) in daughters. We chose to analyze these three components of female reproductive performance because they could be extracted and measured unambiguously for each of the seven primate populations from our comparative life-history dataset. In the aggregate, our results provide important insights into the extent of, and variability in, age-dependent reproductive performance in wild primates.

Results

Interbirth Intervals. Diagnostic checks of the IBI models indicated nonproportional hazards for the effects of female's age and age^2 in most species, and therefore we fit these models using time-varying effects for the age and age^2 terms (*SI Appendix*, Tables S2–S8). In these models, the female's parity status (primiparous vs. multiparous) did not strongly predict time to IBI closure independently of the age and age^2 effects, as in all species the 90% credible intervals of the log hazard ratio for parity included zero (Fig. 1*A*). In contrast, the estimated time-varying log hazard ratios for age revealed a striking pattern in all species except capuchins, such that older females were less likely to close an unusually long IBI by having another offspring (blue lines in Fig. 1*B*, showing that the birth hazards associated with age become more negative over time within each IBI). More simply, as the IBI lengthens, being old is associated with diminishing likelihood of having another offspring and thus closing the IBI in most species.

The time-varying effects of the female's age^2 were also largely consistent across species (except for capuchins and sifakas), such that the log hazard ratios associated with the age^2 term were less than zero early in the IBI (orange lines in Fig. 1*B*). Hence, females at both extremes of the age distribution—both old and young—were more likely to have longer IBIs, especially in muriquis, blue monkeys, baboons, and gorillas. In addition, our models indicate that in all species except capuchins, this effect of extreme age was driven primarily by females in the oldest rather than the youngest age classes; in all but capuchins, the oldest females had substantially longer IBIs and relatively fewer completed IBIs than females at all younger ages (Fig. 2, dark pink lines). In several species—including capuchins, muriquis, blue monkeys, baboons, and gorillas—the youngest females (Fig. 2, dark green lines) also had longer IBIs than middle-aged females, even after accounting for possible effects of primiparity on IBI length.

Offspring Survival. We used proportional hazards models because we found no evidence of time-varying effects for the maternal age variables in the models of offspring survival to age 1 (i.e., nonproportional hazards) (*SI Appendix*, Tables S9–S15). Only in gorillas did the female's parity status (primiparous vs. multiparous) predict infant survival independently of the age and age^2 effects, such that offspring of first-time mothers experienced a higher probability of survival relative to later-born offspring (negative log hazard ratios for parity) (Fig. 3*A*). Sifakas and baboons showed weaker tendencies in the same direction (higher offspring survival in primiparous mothers), whereas blue monkeys showed a tendency in the opposite direction (higher offspring survival in multiparous mothers), but in these and all other species except gorillas, the 90% credible intervals of the log hazard ratio for parity included zero (Fig. 3*A*). In contrast to the weak effects of parity, mother's age or age^2 strongly predicted offspring survival to age 1 in sifakas, muriquis, blue monkeys, and baboons, and to a lesser extent, in gorillas (Fig. 3*A*). The direction of maternal age effects was broadly consistent across species, with markedly lower

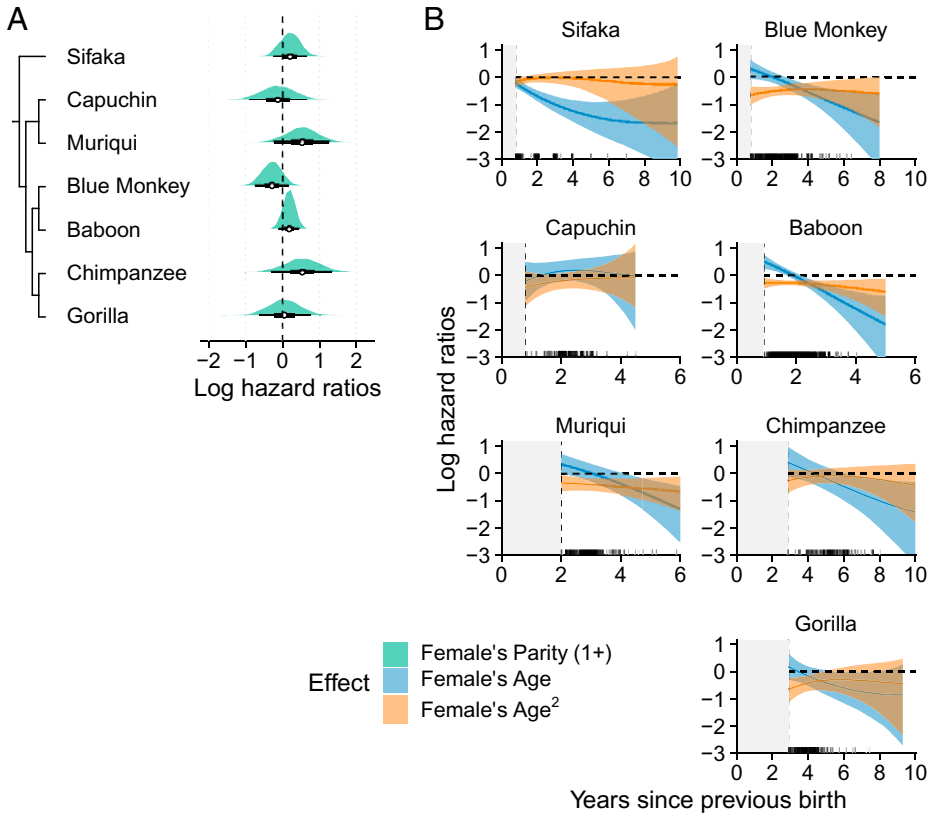

Fig. 1. (*A*) Effect of multiparity versus primiparity on time to IBI closure in each species. Across species, a female's parity status did not strongly predict time to IBI closure. Log hazard ratios greater than 0 indicate that multiparous IBIs tend to be closed faster by a subsequent birth. Shaded areas show posterior densities; white points show medians; thick black bars show 50% credible intervals and thinner black bars show 90% credible intervals of the posterior distributions. (*B*) Time-varying effects of female's age and age^2 in the models of time to IBI closure in each species. Log hazard ratios greater than 0 indicate that higher values of the female's standardized age or age^2 predict shorter IBIs (greater IBI closure hazard). In six of seven species (all but capuchin), old females were less likely to close an unusually long IBI (i.e., the "age" term becomes negative later in the IBI, and the blue line has a negative slope). In addition, in all species except capuchins and sifakas, IBIs were relatively long among the youngest and oldest females, shown by the negative values of "age^2" term. The rug plots show unique event times (i.e., IBIs that were closed by a subsequent birth) for each species. The vertical dashed line shows the minimum uncensored IBI ("time zero") in each species.

offspring survival predicted for very old mothers in these five species (Fig. 3*B*, dark pink lines). In blue monkeys and baboons, we also found reduced survival for offspring of relatively young females, independent of parity (Fig. 3*B*, dark green lines).

Daughter's AFR. Again, we used proportional hazards models because we found no evidence in any species of time-varying effects of maternal age variables (i.e., nonproportional hazards) (*SI Appendix*, Tables S16–S22). In three of seven species, we found no evidence that maternal age or age^2 affected daughters' AFR (Fig. 4*A*). The most notable case in which maternal age did affect daughters' AFR was the muriqui, in which first reproduction was delayed in the daughters of primiparous females (Fig. 4*A*) but otherwise accelerated in the daughters of relatively young multiparous mothers (Fig. 4*B*, green lines). Similar to the pattern in the muriquis, chimpanzees showed weaker tendencies toward delayed first reproduction in the daughters of primiparous females (Fig. 4*A*) and accelerated first reproduction in the daughters of relatively young multiparous females (Fig. 4*B*, green lines). In capuchins and gorillas, we saw some evidence of accelerated first reproduction among the daughters of older mothers (Fig. 4*B*, pink lines). However, sample sizes for AFR were small in chimpanzees, capuchins, and gorillas, and the 90% credible intervals for the maternal age and age^2 terms were wide and included zero.

Discussion

We found evidence for two components of female reproductive senescence in multiple primate species: fertility senescence (IBI) and parental-effect senescence for offspring survival. We also found evidence in some primate species that the youngest mothers experienced longer IBI and lower infant survival. Evidence for an effect of maternal age on the third component we examined, daughter's age at first reproduction (reflecting offspring development), was more mixed. We also documented considerable interspecific variability in the strength and direction of these effects. We find no clear evidence that the heterogeneity across species in these effects was driven by differences between species in sampling of older mothers: Species that showed no evidence of reproductive senescence in a particular outcome did not have noticeably different coverage of mothers in older age classes (*SI Appendix*, Fig. S1).

A Cross-Species Signature of Reproductive Senescence in IBIs. Our analysis of female IBI length over the reproductive lifespan revealed a cross-species signature of fertility decline with old age in six of the seven primate species. The consistency of this pattern was especially striking, with females of the oldest age classes in each species showing trajectories of IBI length that were both longer and less likely to be closed.

Our flexible modeling approach, which allowed maternal age effects to vary over time, also provided new insights into the

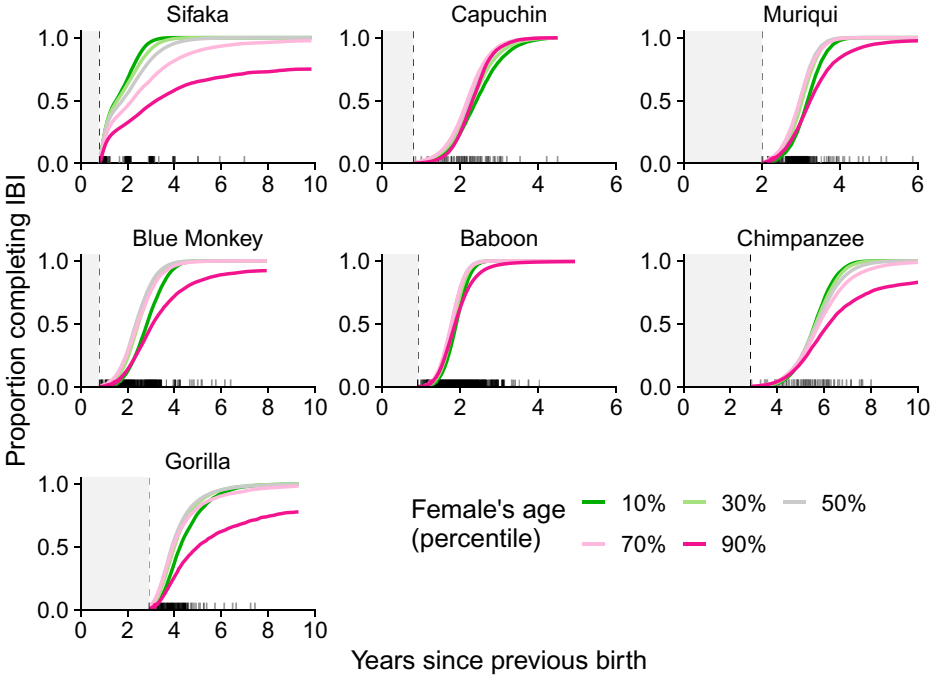

Fig. 2. Model predictions of time to IBI closure for multiparous females of each species (i.e., the IBI opened by a female's first offspring is excluded). In six of seven primate species (all but capuchin), females in the oldest age classes, youngest age classes, or both showed longer IBI lengths than prime-aged females, and the oldest females also showed relatively fewer completed IBIs. The curves represent median predicted probability of closing the IBI for females at different percentiles of the maternal age distribution. The vertical dashed line shows the minimum uncensored IBI ("time zero") in each species. The rug plots show unique event times (i.e., IBIs that were closed by a subsequent birth) for each species.

demographic processes that generate these patterns. For example, if an IBI is unusually long, then age becomes a better predictor of time to IBI closure, or indeed whether the IBI is likely to be closed at all. In the oldest females, for whom mortality risk is high, it becomes increasingly likely as the IBI progresses past a typical length that the IBI will never be closed (i.e., that the mother will die before giving birth again). In contrast, among younger females, the IBI might have been long because of an intervening pregnancy that did not result in a live birth. In these younger females, the probability of eventually closing the IBI with a subsequent live birth remains very high. These processes would explain the time-varying effect of female age on IBI closure: The log hazard becomes negative as older age predicts lower probability of closing an unusually long interval.

Moreover, in most species the time-varying effects of the female's age^2 showed a consistent pattern (orange lines in Fig. 1) in which both the oldest and youngest females were more likely to have relatively long IBIs. Quadratic relationships between maternal age and IBI length or other measures of female fertility have been described previously in our study populations of baboons (43) and blue monkeys (44), as well as in other primate populations, including Japanese macaques (32), semifree-ranging rhesus macaques (45), and a different population of mountain gorillas (34). In addition, previous work showed an effect of primiparity on chimpanzee IBIs such that first-time mothers had longer IBIs (46), an effect that was not evident in our analysis, perhaps because the effect of primiparity was absorbed by our age^2 term. We have also previously reported evidence that female fertility declines with advancing age in several of these species, by examining the probability of live birth (38, 39).

Collectively, these findings point to a shared pattern of reproductive senescence that may be near-universal in species in which mothers invest heavily in relatively few offspring that have a long period of dependence on the mother. Strikingly, the near-universal pattern of reproductive senescence occurs despite large differences among these species in mating systems, life-history schedules, habitat type, breeding seasonality, and social behavior. One likely mechanism underlying reproductive senescence in IBIs is age-related declines in conception rate, most likely as a result of age-related declines in follicular quality. This phenomenon is well-documented in humans (47) and supported by data from baboons (43, 48). Another possible mechanism is age-related increases in early fetal losses, a phenomenon that is well-documented in humans (49); this phenomenon is difficult to detect in primate populations but has been documented in wild baboons (48). In contrast, age does not predict variation in the duration of lactational amenorrhea in baboons, and while age predicts some variation in gestation length in this species, the absolute amount of variation in this phase of the IBI is very small and has little influence on variation in the duration of the overall IBI (43).

The cross-species consistency of how IBI lengths varied with age in six of our seven study species naturally brings focus to the one primate species in our study, the white-faced capuchin, that did not show this pattern. None of the predictors that we considered—female age, age^2, and primiparity status—was a good predictor of time to IBI closure in capuchins. While it is possible that our analysis has identified a genuine absence of longer IBIs in late-aged capuchin females, we consider this scenario unlikely because it would be hard to reconcile both with theory and with the preponderance of empirical evidence showing this pattern in other primate species. Two characteristics of the capuchin fertility data—relatively low sample size and high rates of semistochastic infant mortality associated with drought and male infanticide (50)—caution against overinterpreting this divergent result, because the capuchin models may be underpowered to detect a signature of reproductive aging in IBIs against the backdrop of environmental sources of variance in infant mortality.

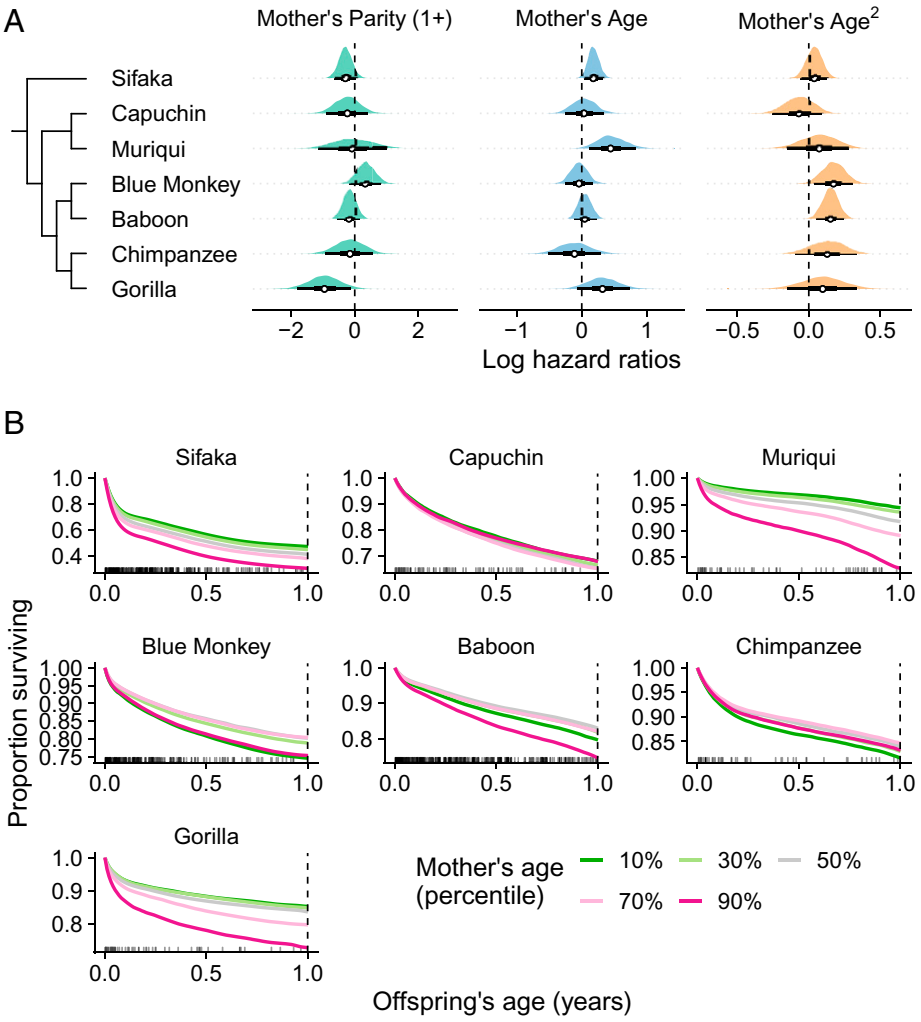

Fig. 3. Survival is markedly lower among offspring of the oldest mothers in five of seven species (all but capuchins and chimpanzees) and also among offspring of the youngest mothers in two of these species (baboons and blue monkeys). (*A*) Modeled effects of mother's parity and mother's standardized age and age^2 on offspring survival to age 1. Positive estimates of the log hazard ratios indicate that being the offspring of a multiparous mother, or higher values of maternal age or maternal age^2, predict greater risk of infant death before age 1. Shaded areas show posterior densities; white points show medians; thick black bars show 50% credible intervals and thinner black bars show 90% credible intervals of the posterior distributions. (*B*) Model predictions of survival to age 1 for offspring of multiparous mothers of different ages. The curves represent median predicted probability of surviving to age 1 for offspring of females at different percentiles of the maternal age distribution. The vertical dashed line shows the enforced censoring time at age 1 for surviving offspring. The rug plots show unique event times (i.e., observed infant deaths) for each species.

Parental-Effect Senescence Revealed by Reduced Infant Survival among Older Mothers in Some Species but Not All Species. Offspring of the oldest mothers were more likely to die within the first year of life in four species—sifakas, muriquis, blue monkeys, and baboons—and there was a tendency in this direction in a fifth species, mountain gorillas. Although not as consistent as the cross-species pattern of IBIs with female age, these findings suggest that parental-effect senescence in the survival of infants is relatively common across primates. Several mechanisms could give rise to this pattern. First, age-related deterioration of gamete quality (13) or reduced provisioning of ova (9) could compromise survival in infants of older mothers. Second, old mothers experiencing somatic decline are more likely to die than younger females before their offspring reach independence, and some of the maternal age effect on infant survival may be due to infant death following loss of the mother. Third, declining somatic state among older mothers could constrain their ability to provide critical care and social support for their infants (11, 27, 51). For example, in five of the seven species studied here, maternal death is preceded by elevated infant mortality, which suggests declining quality of maternal care as the female approaches the end of life (52).

Despite our overarching evidence for parental-effect senescence in offspring survival in most species, our findings agree with previous studies that have not detected a strong signal of maternal age in the infant survival of the same capuchin (53) and chimpanzee (54) populations included in this study. In some species, maternal experience could play an important role in mitigating any association between poor body condition of older mothers and reduced offspring survival. Aging mothers could also lessen the detrimental effects of their own declining somatic state on offspring survival by increasing maternal investment at the cost of future reproduction, given that their future reproductive potential may be low (38). This strategy, known as "terminal investment" (55), has been observed in several long-lived iteroparous animals (27, 56), including nonhuman primates (45, 57). This increased terminal investment is commonly manifested as later age at weaning, but we lack the

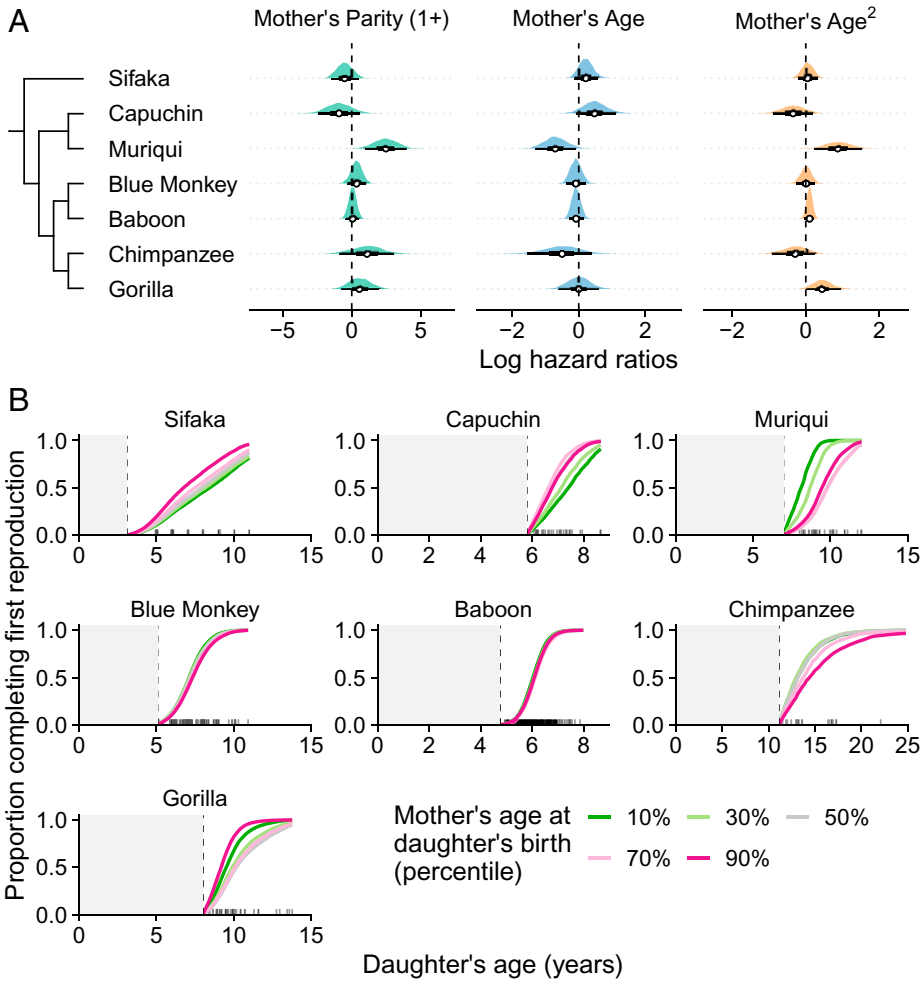

Fig. 4. (*A*) Estimates of the effects of mother's parity, standardized age, and age^2 on the age at which daughters first reproduced in each species. Positive estimates of log hazard ratios indicate that being the daughter of a multiparous mother, or higher values of maternal age or maternal age^2, predict earlier age at first reproduction among daughters. In muriquis, daughters of young mothers in general reproduced earlier, with the exception of daughters of primiparous mothers, who experienced a delay in first reproduction. A similar trend was observed in chimpanzees although the credible intervals overlapped zero. In gorillas and capuchins, the pattern was more ambiguous. In baboons, blue monkeys, and sifakas, maternal age had no effect on the age at which daughters reproduced for the first time. Shaded areas show posterior densities; white points show medians; thick black bars show 50% credible intervals and thinner black bars show 90% credible intervals of the posterior distributions. (*B*) Model predictions of age at first reproduction for daughters of multiparous mothers of different ages. The curves represent the median predicted probability of daughters completing first reproduction for different percentiles of their mothers' age distribution. The vertical dashed line shows the minimum uncensored AFR ("time zero") in each species. The rug plots show unique event times (i.e., completed first reproduction) for each species.

data to test directly whether older mothers in our study species weaned their offspring later. Our finding of markedly longer IBIs among the oldest females in most species is consistent with the possibility that terminal investment occurs in some of these populations, because an extended period of postpartum amenorrhea associated with delayed weaning could contribute to longer IBIs. Alternatively, IBI length may be extended without increased lactational effort if poor body condition among the oldest mothers makes it more difficult for them to recuperate from lactational amenorrhea. More generally, the pattern in multiple primate species in which increasing maternal age is associated with both longer IBIs and lower infant survival raises the question of whether these two components of female reproductive performance are genetically correlated. That is, it may be that parental fitness is maximized when mothers in older age classes increase their investment in their offspring (by lengthening IBI) and thereby enhance infant survival, even if the longer IBIs do not fully offset the survival cost to infants of having an older mother (58). The nature and consequences of these within-species correlations between components of maternal reproductive performance is a high priority for future research.

Another possible explanation for the lack of a maternal age signal in infant survival for some species is a high degree of infant mortality linked to semistochastic environmental conditions. High environmentally driven infant mortality will reduce the maternal age signal-to-noise ratio, particularly in species with relatively low sample sizes. These conditions likely pertain to the capuchin population, in which infanticide (59–61) and drought (50) are major sources of infant mortality that have irregular temporal patterning.

Increased infant mortality in primiparous females has been described in several primate populations (30–33), with notable exceptions (e.g., ref. 62). Among our study species, previous studies have identified the lack of firstborn disadvantage in chimpanzees (54), blue monkeys (63), and a different population of mountain gorillas (34). In chimpanzees, Stanton et al. (54), argued that primiparous females successfully compensate for their inexperience and low social status by increasing

Table 1. Summary of hierarchical survival models used to analyze maternal age effects on IBI length, offspring survival to age 1, and daughter's age at first reproduction

Event	Fixed effects	Random effects
IBI (interbirth interval completion)	Female's age (time varying) Female's age^2 (time varying) Female's parity (0 vs. 1+)	Female's ID Social group in which the birth that opened the interval occurred Year of birth that opened the interval
Offspring survival to 1 y of age	Age of offspring's mother Age^2 of offspring's mother Parity of offspring's mother (0 vs. 1+)	ID of offspring's mother Social group into which offspring was born Year of offspring's birth
AFR (daughter's age at first reproduction)	Age of daughter's mother Age^2 of daughter's mother Parity of daughter's mother (0 vs. 1+)	ID of daughter's mother Social group into which daughter was born Year of daughter's birth

investment in firstborn offspring. Extended IBIs in primiparas could also result from differences in body condition, for example if relatively low body weight in primiparas makes their recuperation time from lactational amenorrhea longer compared to females in their prime reproductive years. Our findings bolster previous cross-species surveys indicating that firstborn disadvantage is not universal across primates, and that species-specific compensatory mechanisms may partly explain this result (35).

Mixed Evidence for Parental-Effect Senescence Affecting AFR Next Generation. In contrast to the strong cross-species signals of age in female IBIs and offspring survival, we found mixed evidence for parental-effect senescence in the AFR of the next generation. Mother's age or age^2 failed to predict daughter's AFR in three of our study species: baboons, blue monkeys, and sifakas. Among the four species in which there was moderate to reasonably strong evidence for maternal age effects—capuchins, muriquis, chimpanzees, and gorillas—the direction of the effects of maternal age and age^2 were not consistent. We might expect age at first reproduction to be less plastic than survival, and hence less subject to parental effects, because of its strong correlation with lifespan across species (64, 65). It is noteworthy, however, that similar patterns of delayed first reproduction in the daughters of primiparous females and accelerated first reproduction in the daughters of relatively young, multiparous females were evident in both muriquis and chimpanzees. Among our seven study species, only these two have routine female-biased dispersal in which maturing females typically disperse to a new social group before first reproduction. Previous studies suggest a shared mechanism for early AFR among the daughters of younger mothers, after accounting for the effects of primiparity: Daughters experience accelerated maturity when they reproduce in their natal group, in which their mother is usually present, compared to females who disperse to a new social group in both muriquis (66) and chimpanzees (67). Because of the relatively long time to maturity in both species, this situation is more likely to occur among the daughters of relatively young mothers, if older mothers are more likely to die before their daughters could reach sexual maturity.

Previous research in several of these primate populations has found that female AFR is sensitive to a variety of social and ecological conditions. For example, maternal social status and the quality of the early-life environment are also known to affect age at sexual maturity in baboons (68) and AFR in several other primate taxa (69). In chimpanzees, female AFR depends on social conditions—including mother's rank, being orphaned, and dispersal status (67)—but in gorillas, which have bisexual dispersal, female dispersal status prior to first parturition does not affect AFR (70). We did not include socio-ecological factors in our analysis of AFR because such contextual data were generally not contained in the primate life-history database. Nonetheless, the lack of a consistent effect of maternal age in our analysis combined with the lack of an overarching trend in the literature argue against a cross-species signature of parental-effect senescence in the AFR of daughters.

Conclusions. In summary, we found a cross-species signature of female reproductive aging among nonhuman primates that takes the form of longer IBIs among old-aged females in six of our seven study species. In addition, in most of our study species, middle-aged females had shorter IBIs compared to females that were very young or very old. We found more limited, species-specific evidence of maternal age effects on components of fitness in the next generation. Parental-effect senescence, a negative relationship between mother's age and offspring fitness, was manifested as later age at first reproduction among the daughters of older muriquis and chimpanzees, and as reduced infant survival among the offspring of older mothers in sifakas, muriquis, blue monkeys, baboons, and mountain gorillas.

Recent comparative analyses of aging in humans and nonhuman primates have challenged long-standing assumptions about the uniqueness of human life histories. On the one hand, cross-species comparisons indicate that age-specific trajectories of mortality in humans lie in a continuum with our nonhuman primate relatives (37, 40, 71–73). On the other hand, the pattern of female reproductive aging in humans, in which women experience fertility cessation in midlife prior to the acceleration of somatic decline, is unique among primates (38). Our findings shed new light on the patterns and consequences of female reproductive aging in nonhuman primates, revealing shared patterns and contrasts across species in female fertility senescence and parental-effect senescence. These observations call for further cross-species comparative analyses of reproductive aging, as well as studies of male reproductive aging, to improve our understanding of the evolution of human life-history patterns.

Materials and Methods

Study Populations. The seven primate species included in this study represent four major radiations of primates. They include: one strepsirrhine, Verreaux's sifakas (*Propithecus verreauxi*); two platyrrhines, white-faced capuchins (*Cebus capucinus imitator*) and northern muriquis (*Brachyteles hypoxanthus*); two cercopithecoids, blue monkeys (*Cercopithecus mitis stuhlmanni*) and yellow baboons (*Papio cynocephalus*); and two great apes, eastern chimpanzees (*Pan troglodytes schweinfurthii*) and mountain gorillas (*Gorilla beringei beringei*). The life-history data provide biographical information for 5,219 individual animals and reproductive information for 1,949 individual females. Strier et al. (36) recount the

creation of the Primate Life History Database (PLHD, http://demo.plhdb.org/) that comprises these data. Biographical data include sex, date of birth, mother's identity (if known), the date and way in which each animal entered and departed the study, and whether the individual was known with certainty to be the mother's firstborn offspring. Female reproductive data include periods during which each female's fertility was continuously monitored. Because the PLHD only contains life-history data and maternity information, we are not able to measure all aspects of female reproductive performance; for example, the PLHD does not contain information about birth weight, weaning, growth rates, or health. Sample sizes for each of the three analyses described here are shown in *SI Appendix*, Table S1, and the distributions of maternal ages for completed intervals of each outcome are shown in *SI Appendix*, Fig. S1. Permission for the primate field studies was provided by the governments of Brazil, Costa Rica, Kenya, Madagascar, Rwanda and Tanzania. Research protocols complied with all institutional animal care and use committee guidelines and adhered to the laws and guidelines in the host countries.

Data for Analysis of IBIs. Our goal was to predict how a female's age, combined with other predictors, affected the duration of her IBIs (Table 1). We treated the dataset of IBI closures as failure time data that were right-censored, and we modeled time to IBI closure (time from one live birth to next live birth for each adult female) by using a survival model and including female age as a predictor.

For the analysis of IBI length, we applied a set of inclusion criteria that are shown in *SI Appendix*, Fig. S2. Two types of IBIs contributed to the analysis: 1) completed IBIs, which were intervals that were both opened and closed by sequential live births; and 2) censored IBIs, which were intervals that were opened by a live birth but that remained unclosed by a subsequent birth by the time observations ceased. We discarded all cases in which the IBI was shortened by the early death of the infant that opened the interval. We considered early death to have occurred if both of two conditions were met: 1) the first offspring died before the next sibling's most likely conception date, which we defined as the second offspring's date of birth minus the species' average gestation length; and 2) the first offspring died before an expected date of next conception based on the population median IBI length minus the average gestation length. The second criterion was included to avoid discarding long IBIs in which the first offspring died after weaning but before the next offspring's estimated date of conception. In rare cases of twins (16 total cases, for 32 individual offspring), the date of death or censoring for the last-surviving twin was used to determine whether the IBI was shortened. For example, an IBI in which only one twin survived to the next offspring's date of conception would not be considered shortened and would be retained in the analysis.

In the survival models of IBI closure, we defined time 0 for each IBI as the date of birth of the offspring that opened the interval plus the minimum uncensored IBI for the species. Time 0 is therefore species-specific, and represents the shortest duration at which any IBI for a given species was closed. It thus marks the start of the "risk period" for IBI closure for each species. For completed (uncensored) IBIs, the time variable in the survival models was calculated as time elapsed between the date at time 0 and the date of IBI completion. For censored IBIs, the time variable was calculated as the time elapsed between the date at time 0 and the date at the female's departure from the study or the end of the study period (e.g., by death, disappearance, or right censoring).

Data for Analysis of Offspring Survival to Age 1. Our goal was to determine how a female's age affects the survival of her offspring. The data inclusion process and criteria for the analysis of offspring survival to age 1 are shown in *SI Appendix*, Fig. S3. Completed survival intervals were those in which the offspring died before 1 y of age. In the survival models, the time variable for completed survival intervals was the offspring's age in days on the date of death. There were two types of censored survival intervals. First, an offspring's survival information could be censored by the end of observations before reaching 1 y of age. In these cases, the time variable was the offspring's age in days on the date of censoring. Second, an offspring could survive to 1 y of age, in which case the offspring's death was not observed for the purposes of this analysis. In these cases, the time variable was equal to 1 y.

Data for Analysis of AFR for Females. For each female in each species, the PLHD provides 1) the age of her mother at the female's birth, and 2) the date of birth for the female's first live-born offspring, if known. Our goal, for each female in the dataset, was to determine the effect of her mother's age at the time of the female's birth on her own AFR. As with the analysis of IBI, we treated AFR as failure time with right-censoring, and we modeled AFR using a survival model, including the age of each female's mother as a predictor of that female's AFR. The sequence of inclusion criteria that we applied for the analysis of AFR for females is shown in *SI Appendix*, Fig. S4. If known, the date of birth of her first live-born offspring is taken as that female's AFR. Any parous females for which the first live birth is unknown were excluded from the analysis. Specifically, females were excluded if they entered the study after adulthood, or if their fertility status was not monitored continuously so that they could have experienced an unrecorded first live birth. Censored ages at first reproduction were those in which a female had not yet experienced her first live birth when observations ceased, and they were assigned only when the female entered the study as an immature animal and her fertility was monitored from her date of entry to the date of censoring. We excluded females that met the criteria listed above but whose age at first reproduction nonetheless had high uncertainty (>6 mo).

In the models of female AFR, we defined time 0 for each female–the start of the "risk period" for AFR completion–as that female's date of birth plus the minimum uncensored AFR for the species. Hence, the time variable in the survival models of AFR completion was calculated for each female as the time elapsed between the date at time 0 and the date of her first live-born offspring's birth (for uncensored intervals) or the date of censoring.

Statistical Models. We used hierarchical models for clustered survival data to analyze how maternal age and parity influence time until the occurrence of our events of interest. Survival models reduce well-known biases that emerge from ignoring censored intervals in analyses of demographic outcomes (74, 75). The hierarchical structure of our models allows us to account for individual heterogeneity and uneven sampling among clustering units in the models when making inferences about the effects of maternal age and parity status on the reproductive outcomes. Specifically, the random effects or "frailty terms" in the models (Table 1) estimate the variance attributable to correlations among multiple time-to-event intervals that occur within the grouping factors of particular mothers, social groups, and years (*SI Appendix*, Figs. S5–S7).

For each outcome and species separately, we fit flexible parametric survival functions in which the baseline hazard was modeled as a smooth function of time using splines. Each model included mother's age, mother's age^2, and mother's parity status (primiparous vs. multiparous) as fixed effects, as well as the random effects listed in Table 1. We standardized mother's age within species before squaring to increase independence of the linear and quadratic terms and to improve interpretability of the coefficients (76). Specifically, after centering, the estimate for the linear age term conveys whether older mothers have higher hazard values for the response, while the estimate for the quadratic age term conveys whether extreme-aged mothers, either very young or very old, have higher hazard values for the response in addition to any linear relationship. Diagnostic checks of the models revealed some violations of the proportional hazards assumption for a standard Cox regression model. Specifically, in some models of IBI length (but not other reproductive outcome variables), the effect of the maternal age variables on the event hazard was not constant but rather changed as a function of time since the beginning of the timeline to the event (e.g., time since opening an IBI). Therefore, in the models of IBI length we allowed for time-varying effects of the age covariates, in which the time-varying log hazard ratio was modeled using cubic B-splines with boundary knots positioned at the limits of event times. We used the R statistical computing environment for all analyses (77), and we fit all models using the survival analysis development branch of the R package rstanarm found in ref. 78 (see also refs. 79 and 80). We used weakly informative (default) priors and fit the models using four Markov chains and 2,000 iterations. We ensured appropriate chain mixing in each model by verifying that values of the potential scale reduction statistic Rhat were less than 1.1 for all parameters.

Data Availability. CSV file data have been deposited in the Duke University Research Data Repository (https://doi.org/10.7924/r4pn9600q) (81).

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