

Higher early life mortality with lower infant body mass in a free-ranging primate

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Abstract

1. Traits that reflect the amount of energy allocated to offspring by mothers, such as infant body mass, are predicted to have long-lasting effects on offspring fitness. In very long-lived species, such as anthropoid primates, where long-lasting and obligate parental care is required for successful recruitment of offspring, there are few studies on the fitness implications of low body mass among infants.
2. Using body mass data collected from 253 free-ranging rhesus macaque *Macaca mulatta* infants on Cayo Santiago, Puerto Rico, we examined if lower infant body mass predicts lower chance of survival through to reproductive maturation (4th year of life). We also used data on inter-birth intervals and suckling behaviours to determine whether the duration of maternal care was adjusted to infant body mass.
3. Rhesus macaque infants experienced on average 5% reduced hazard of death for an increase in body mass of 0.1 SD (~100 g) above the mean within their age–sex class. The positive association between body mass and early life survival was most pronounced in the 1st year of life.
4. Infant body mass tended to be lower if mothers were young or old, but the link between infant body mass and early life survival remained after controlling for maternal age. This finding suggests that maternal effects on early life survival such as maternal age may act through their influence on infant body mass.
5. Mothers of heavier infants were less likely to be delayed in subsequent reproduction, but the estimated association slightly overlapped with zero. The timing of the last week of suckling did not differ by infant body mass.
6. Using infant body mass data that has been rarely available from free-ranging primates, our study provides comparative evidence to strengthen the existing body of literature on the fitness implications of variation in infant body mass.

KEYWORDS

early life survival, free-ranging animals, infant body mass, maternal investment, primates, rhesus macaques

1 | INTRODUCTION

Measures of parental care, such as infant body mass at or immediately following birth, are important predictors of lifetime reproductive success for both sexes in many species of vertebrates (Lindström, 1999; Lummaa & Clutton-Brock, 2002) and invertebrates (e.g. burying beetles; Smith, 2002). Studies have shown that infant body mass predicts early life survival, as well as traits such as adult body size, which predict fecundity (Catchpole, Fan, Morgan, Clutton-Brock, & Coulson, 2004; Loison, Langvatn, & Solberg, 1999; Maniscalco, 2014; McMahon, Burton, & Bester, 2000; Pélabon, 1997; Small & Smith, 1986; Terry, Ferris, Tehranifar, Wei, & Flom, 2009). The link between infant body mass and early life survival has been of particular interest in studies of long-lived iteroparous species. Here, because survival rate is lower during early life, but temporally more variable than adult survival (Fowler & Smith, 1981), variation in early life survival often accounts for a significant portion of later fitness outcomes and population dynamics (Clutton-Brock, 1988; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000). Previous studies have examined infant body mass in an effort to understand the sources of variation in early life survival and its implications for population biology and demography, mostly based on data from large herbivores (Albon, Clutton-Brock, & Guinness, 1987; Clutton-Brock, Price, Albon, & Jewell, 1992; Festa-Bianchet, Jorgenson, & Réale, 2000; Gaillard et al., 1997; Steinheim, Mysterud, Holand, Bakken, & Ådnøy, 2002).

Few data are currently available to test whether infant body mass predicts early life survival in very long-lived species such as anthropoid primates, outside of humans (McCormick, 1985; Paneth, 1995; Watkins, Kotecha, & Kotecha, 2016), in which complex sociocultural factors such as variation in diet and access to healthcare often confound life-history variation. Primate life history is characterized by a particularly critical trade-off between fecundity and early life survival, reflecting the slow growth and extended dependence of offspring on parental care compared with other mammals of similar size (Charnov & Berrigan, 1993; Jones, 2011). Minimizing mortality during early life is thus expected to have been an important force shaping the evolution of life history in primates (Altmann, 1998; Janson & van Schaik, 2002). In ensuring the survival of offspring to reproductive age, the maternal environment plays a critical role and exhibits a particularly long-term influence on offspring fitness in primates (Altmann, 1998; Lee, 1996; Maestriperi, 2018; van Noordwijk, 2012; Silk, Alberts, & Altmann, 2003). Studies in primates have shown that, not only does the maternal environment underlie the variation in infant body mass via maternal effects (Altmann & Alberts, 2005; Garcia, Lee, & Rosetta, 2009; Hinde, 2007; Johnson, 2003; Maestriperi, 2009; Nuñez, Grote, Wechsler, Allen-Blevins, & Hinde, 2015; Setchell, Lee, Wickings, & Dixon, 2001) but also the duration of maternal care acts as a facultative adjustment to developmental cues from their infants, such as changes in body mass (Bowman & Lee, 1995; Garcia, 2014; Reitsemá, Partrick, & Muir, 2015). Clarifying the fitness implications of variation in infant body mass could help better

understand the dynamics between offspring development and maternal care. However, due to the difficulty of obtaining weight measurements from young individuals in free-ranging settings, few studies of primates have tested the link between infant body mass and early life survival. Those that have so far are limited either by a small sample size (Altmann & Alberts, 2005) or by being undertaken in captive settings (Jaquish, Tardif, & Cheverud, 1997; Nuñez et al., 2015; Small & Smith, 1986).

In this study, we present data from the free-ranging population of rhesus macaques *Macaca mulatta* on Cayo Santiago, Puerto Rico, where weight data can be collected during trapping periods, and for which demographic data on births, deaths, and group membership of all animals on the island have been updated daily over the last 60 years. Observations on social interactions have been conducted on subsets of animals, allowing for the accumulation of behavioural data on dominance rank and mother-offspring interactions. Although the population is free of natural predators and is partially provisioned (Marriott, Roemer, & Sultana, 1989), there is as yet no evidence that basic behavioural traits have been modified substantially on the island, and the situation allows life history and demographic data to be collected with a great deal of regularity and rigor (e.g. Bercovitch, 1997; Bercovitch et al., 2003; Blomquist, 2013; Hernández-Pacheco et al., 2013; Rawlins & Kessler, 1986; Sade, 1990).

Here, utilizing matched body mass data, demographic, and behavioural data from a large number of individuals, we aimed to better understand the functional consequences of variation in infant body mass in primates. To understand the fitness consequences of infant body mass in both offspring and mother, we undertook two sets of analyses. First, we asked: Does infant body mass predict early life survival? We predicted that heavier infants benefit from a higher chance of survival to reproductive maturation (4th year of life), after adjusting for other variables that potentially influence early life survival in primates. Second, we asked: Is the duration of maternal care related to infant body mass, as measured by time to subsequent reproduction or cessation of suckling? If infant body mass predicts early life survival, we predicted that mothers would provide care for longer to offspring who exhibit lower infant body mass, even if the longer care entails a delay in a mother's subsequent reproduction (Bateson, 1994; Lee, 1996; Lee, Majluf, & Gordon, 1991). For example, in a study on wild chacma baboons *Papio ursinus*, low-ranking females tended to wean their smaller offspring later, potentially as a compensatory allocation so that their offspring reach similar weight at weaning as offspring of high-ranking females (Johnson, 2003). To control for differences in maternal conditions that may affect the degree of maternal care in anthropoid primates, we considered maternal age, primiparity, and dominance rank in addition to infant body mass (Altmann, 1980; Bercovitch, Widdig, & Nürnberg, 2000; Berman, 1992; Fairbanks & McGuire, 1995; Gagliardi, Liukkonen, Phillippi-Falkenstein, Harrison, & Kubisch, 2007; Garcia, 2014; Gomendio, 1991; Hoffman, Higham, Mas-Rivera, Ayala, & Maestriperi, 2010; Rosetta, Lee, & Garcia, 2011; Silk, 1988).

2 | MATERIALS AND METHODS

2.1 | Study site

The present study took place on Cayo Santiago, a 15.2 ha island located 1 km off the South-East coast of Puerto Rico. Rhesus macaques were introduced to the island in 1938, with continuous demographic data collected since 1956 (Kessler & Rawlins, 2016). All animals are identified individually and data on births, deaths, reproductions, and dispersal are updated daily (Monday–Friday) by the census team of the Caribbean Primate Research Center (CPRC). Animals are provisioned with commercial monkey chow once every morning and provided with water ad libitum, but have historically spent up to a maximum of ~50% of their feeding time foraging on natural vegetation (Marriott et al., 1989). The monkeys live in naturally formed social groups with evidence of inbreeding avoidance (Widdig et al., 2017). Rhesus macaque females breed every year or every other year, as they exhibit reproductive synchrony at an approximately yearly interval (Hernández-Pacheco, Rawlins, et al., 2016; Vandenberg & Vessey, 1968). As a consequence, there is a 6-month mating season followed by a 6-month birth season on Cayo Santiago. Rhesus macaques form multi-male and multi-female groups and mate with multiple partners (Southwick, Beg, & Siddiqi, 1965). During the study period (2005–2008 and 2011), the island was populated by ~1,200 rhesus macaques living in six groups. The animals are not handled outside of an annual 2-month trapping period, which usually overlaps with the transition between birth and mating seasons. During trapping periods, animals are captured to mark all yearlings with an individual tattoo and ear notches, to obtain their blood samples for the genetic pedigree, and to remove some individuals for population control. As a result of density-dependent feedback on fertility caused by the removal of adult females (Hernández-Pacheco, Delgado, et al., 2016; Hernández-Pacheco et al., 2013), the Cayo Santiago population has exhibited high population growth. Of note, previous observations on un-provisioned macaques also found a fast population growth (e.g. Japanese macaques *Macaca fuscata*; Fedigan, Gouzoules, & Gouzoules, 1983) and even more rapid population growth than that on Cayo Santiago (rhesus macaques at Tughlaqabad in India; Malik, Seth, & Southwick, 1984). The present study analytically controls for potential effects of yearly changes in population dynamics on life-history traits by incorporating year as a random effect in mixed-effects models throughout the analyses (see below).

2.2 | Subjects and data collection

2.2.1 | Infant body mass: Relative body mass within age–sex class

Infant body mass data were collected as part of projects led by AW, TM, and CD. The present study is based on data from 253 infants (122 females and 131 males) who were weighed between 0 and 4.5 months postpartum. The data for 50 of these individuals have

been used in one prior analysis on a different topic (Langos, Kulik, Ruiz-Lambides, & Widdig, 2015); the rest is previously unpublished. The period of 0–4.5 months postpartum precedes a typical weaning period of 5–10 months in rhesus macaques as estimated by nutritional transition away from milk (Austin et al., 2013; Bowman & Lee, 1995; Reitsema et al., 2015), maternal resumption of cycles and ovulation (Berman, Rasmussen, & Suomi, 1993; Gomendio, 1989; Wilson, Walker, Pope, & Gordon, 1988), and a peak in maternal rejection and change in mother–infant contact (Hinde & Spencer-Booth, 1967). Infants were captured with their mothers and weighed while awake to the nearest 0.01 kg while their mothers were anesthetized with an injection of ketamine (10 mg/kg per body weight). Capturing and anesthetization were conducted by trained veterinarian personnel of the CPRC. Because the infants were weighed at random ages between 0 and 6 months, we ran a linear regression on raw body mass values using sex, age (days) at measurement, and the interaction between the two. As body mass increases linearly during this period (Small & Smith, 1986), we did not include a quadratic term for age. The obtained regression formula was $0.650 + 0.002 \times \text{age} - 0.100 \times \text{male} + 0.001 \times \text{age} \times \text{male}$ (Supporting Information S1). We then took residuals, which reflect relative infant body mass within each age–sex class, and used the standardized residuals as measures of infant body mass in all analyses.

2.2.2 | Early life survival: Survival to reproductive maturation

Four-years old is the average age in the population at which a female rhesus macaque starts reproduction and at which a male rhesus macaque begins to disperse from natal groups, although they can start reproducing at 3 years of age (Bercovitch, 1997; Bercovitch et al., 2003; Pittet, Johnson, & Hinde, 2017). Based on the CPRC demographic database, we calculated age (in days) at which each subject was observed for death or was censored (either survived past or removed from the island).

2.2.3 | Duration of maternal allocation: Birth skipping and the cessation of suckling

We used two proxies of the duration of maternal allocation of resources to current offspring—whether subsequent reproduction was delayed for more than a year (birth skipping), and the offspring age at which their suckling behaviours have ceased (cessation of suckling). In seasonal breeders, where females can conceive only during a limited window of time in a given mating season, birth skipping represents the reproductive life costs created by investment in the current offspring at the expense to the mother of transition to the next bout of reproduction. Despite the costs that birth skipping brings by delaying subsequent reproduction, it nonetheless may be an optimal strategy if the delay improves the viability and future fitness outcomes of offspring (Altmann, 1983; Silk, 1990). In the rhesus macaques of Cayo

Santiago, juvenile survival is higher if a younger sibling is born after more than a year, that is, if the mother 'skips' at least a year before conceiving her next offspring (Lee, Ruiz-Lambides, & Higham, 2019). If longer maternal care could improve offspring viability, then an optimal maternal allocation strategy would be to delay subsequent reproduction for offspring with lower expected fitness, for example, lower infant body mass. To test whether maternal reproduction is indeed delayed more than a year if the current offspring exhibits a low body mass, we assessed whether a sibling was born in the following breeding year for each of the subjects, based on information from the CPRC demographic database. Whether birth skipping is due to a lack of conception or because of conception and subsequent miscarriage is unknown for each case, but the consequence would be the same in that the current offspring receives a longer care and subsequent reproduction is delayed for the mother.

Suckling is a behaviour by which primate mothers allocate resources to their current offspring, and lactation is an energetically costly period in mammalian female reproduction. In anthropoid primates, lactating females lose more weight, experience heightened mortality risk, and are delayed in wound healing, when compared with non-lactating females (Altmann, 1983; Archie, Altmann, & Alberts, 2014; Bercovitch, 1987; Hoffman et al., 2008; Rosetta et al., 2011). We used the total duration of suckling as a measure of the amount of post-parturition maternal care in current offspring. Behavioural data were obtained in 2011 from a prior study (Mandalaywala, Higham, Heistermann, Parker, & Maestripietri, 2014). Briefly, observational data on maternal and infant behaviours, including suckling behaviour, were collected using continuous focal animal sampling, during a 30-min weekly session from birth (Mandalaywala et al., 2014). To determine when suckling declined, we examined behavioural data 5–12 months of age when weaning is most likely in rhesus macaques (see above Section 2.2.1) and used a cut-off for a decline in infant suckling as being 2 bouts or less per observed hour for 3 consecutive weeks, based on a previous study on captive rhesus macaques showing that suckling frequency of less than twice an hour during the mating season distinguished mothers who reconceived from those who did not (Gomendio, 1989). We defined a bout of suckling as a continuous suckling behaviour (nipple in mouth with jaw movement) separated by more than a minute from a previous suckling bout or following access to the nipple (Gomendio, 1989). Because data were only available on a weekly basis, age at cessation of suckling was processed in week-age units. The estimated last week of suckling for the study subjects was on average (mean) 45.8 weeks postpartum (max = 60, min = 28, 95% CI = 45.4–46.2), which was a median 9.1 weeks before the birth of the next sibling (max = 28 weeks, min = 2 days). This observation suggests that suckling continued into gestation, since gestation length is 23–24 weeks on average in rhesus macaques (Silk, Short, Roberts, & Kusnitz, 1993).

2.2.4 | Other variables

We considered variables that are known or predicted to influence early life survival or the duration of maternal allocation in

rhesus macaques and primates in general. These include maternal age (years; linear and quadratic), primiparity (whether or not current offspring is the first offspring), and maternal dominance rank (high/middle/low). We chose to include linear and quadratic terms of maternal age, based on previous findings that offspring survival is lower for mothers who are either very young or very old in rhesus macaques (Blomquist, 2013; Gagliardi et al., 2007; also see Supporting Information S2 for the quadratic relationship between maternal and survival until the 4th year of life in the present dataset). For the duration of maternal allocation, we additionally considered birth timing, which reflects how relatively early or late an offspring was born in a given birth season. Birth timing in seasonally breeding species is known to influence how much a mother can allocate resources to current offspring (Berman, Rasmussen, & Suomi, 1994; Fürtbauer, Schülke, Heistermann, & Ostner, 2010; Vandeleeest & Capitanio, 2012) because reproductive synchrony in the study species constrains individual time schedules for reproductive transition and as such, infants born later during a birth season will be relatively immature at the beginning of a mating season. The birth timing variable was calculated as the difference (in days) between the birth date of current offspring and the median birth date of a birth season. We also accounted for the nesting of each infant within mothers (maternal ID) and birth cohort (born during the same birth season) independently.

All of the above variables, except for maternal dominance rank, were extracted from the CPRC demographic database. Maternal rank information was contributed by studies in which the methods for rank assessment are described (Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011; Langos et al., 2015; Mandalaywala et al., 2014). Briefly, aggression and submission events between female adult macaques were recorded, and a linear hierarchy was established which were confirmed to be stable over time. Dominance rank positions of the mothers whose behavioural data were not collected were inferred using the assumption of youngest ascendancy, in which younger siblings acquire higher ranks (Datta, 1988; Kawamura, 1965). Individuals were then divided into three evenly sized low, middle, and high rank groups.

2.3 | Analysis

We used R version 3.4.2 (R Development Core Team, 2018) for data processing, statistical analysis, and visualization. Our analytic approach is explained in detail below.

2.3.1 | Analysis 1: Does infant body mass predict early life survival?

We analyzed survival up to the 4th year of life using mixed-effects Cox proportional hazards models (Austin, 2017; Therneau & Grambsch, 2013), which account for potential heterogeneities in early life survival by mothers and by birth cohorts. A total of 234

infants were available with information matched for infant body mass, maternal age, primiparity, and dominance rank. Because the proportional hazards (P-H) assumption was not met for the infant body mass variable in an initial hazards model, suggesting that the link between infant body mass and offspring mortality changes over time, we extended the model by stratifying infant body mass into three epochs (birth to 1 year, 1–1.5 years and 1.5–4 years) after inspecting the estimated coefficient for infant body mass by time. This approach allowed us to identify how the link between infant body mass and early life survival changes across different age periods. The resulting stratified Cox model satisfied the P-H assumption (Supporting Information S3).

The estimated coefficients reported are shrinkage estimators fitted using a joint shrinkage method. We took this approach as an alternative to model selection, which is not desirable for models with binary outcomes if the events-per-variable (EPV) ratio—the ratio of the number of events (deaths or birth skipping in the present study) to the number of independent variables considered—is lower than a minimum of 5–10 needed to ensure model stability (Heinze & Dunkler, 2017; Heinze, Wallisch, & Dunkler, 2018). Although a low EPV ratio would not increase estimate bias if the sample size is sufficiently large (van Smeden et al., 2016), as is the case in the present study, it would decrease model stability if variable selection is conducted. In cases of low EPV, the literature on variable selection suggests that we should not subject independent variables to selection but instead estimate a global model (i.e. including all variables of interest) with shrinkage factor, which prevents over-fitting of data by ‘shrinking’ extreme values towards central value. For fitting the models, we used the R packages *SURVIVAL* v.2.41-3 (Therneau & Grambsch, 2013), *COXME* v.2.2-10, and *SHRINK* v.1.2.1 (Dunkler, Sauerbrei, & Heinze, 2016).

2.3.2 | Analysis 2: Is the duration of maternal care related to infant body mass?

To test whether the duration of maternal care acts as a facultative adjustment to infant body mass, via either increased probability of birth skipping or delayed week-age at the cessation of suckling, we used for the former a GLMM with logit link for the binary response variable, and for the latter a GLM. Note that no mixed-effects model was considered for the latter because the behavioural data on suckling did not include repeated measures from the same mother and were all from one birth cohort. In each of the GLMM and GLM, we considered fixed-effects of infant body mass, birth timing, maternal age, primiparity, and dominance rank. The numbers of infants available with matched information on these fixed-effects variables and respective response variables for GLMM and GLM were 217 and 38, respectively.

For the same reason as explained above for the hazards model, we did not conduct variable selection for the GLMM due to the low EPV and instead sought to estimate the global model with shrinkage factor. We fitted the GLMM using a Markov chain Monte Carlo

(MCMC) technique which implicitly implements shrinkage in parameter estimation. We used weakly informative priors and conducted 2,000 iterations (half discarded as ‘warm-up’) for each Markov chain, and then assessed convergence and sampling quality using split- \hat{R} and effective sample size (Supporting Information S4). For modelling the last week of suckling, no issue of EPV ratio is present because the outcome is not binary. Here, we subjected the LM to backward model selection to test whether the best model retains the infant body mass variable. We used the R packages *RSTANARM* (Stan Development Team, 2016) v.2.18.2 for the GLMM and *LME4* (Bates, Mächler, Bolker, & Walker, 2015) v.1.1-21 and *MASS* (Venables & Ripley, 2013) for the GLM.

3 | RESULTS

3.1 | Does infant body mass predict early life survival?

Of the 234 infants studied, 15 died within the 1st year of life and a further 15 died before they reached 4 years. Early life survival was more likely for infants with heavier body mass, but the relationship was clear only during the 1st year of life (Table 1). During this period, the hazard of death reduced on average by 4.9 (95% confidence

TABLE 1 Early life survival in the rhesus macaques of Cayo Santiago ($N = 234$). Estimates are bolded when their 95% CI's do not overlap with one (i.e., equivalent to zero for un-exponentiated coefficients)

	Coefficient estimate ^a		95% CI	
	e^{β}	SE	Lower	Upper
Body mass: 0–1st year	0.51	0.18	0.36	0.72
Body mass: 1–1.5th year	0.73	0.19	0.51	1.05
Body mass: 1.5–4th year	1.14	0.15	0.86	1.53
Maternal age (linear)	1.17	0.15	0.87	1.56
Maternal age (quadratic)	1.09	0.10	0.90	1.31
Maternal rank: middle	1.50	0.27	0.88	2.55
Maternal rank: low	1.51	0.26	0.90	2.53
Primiparity	1.20	0.43	0.46	2.50

^aIn hazards models, the exponentiated value of an estimated coefficient represents the change in the expected hazard ratio relative to a unit change the variable. Hazard refers to an instantaneous, as opposed to cumulative, rate of event at some time point t given that the event did not occur up to time t . Since we calculated time in days as a unit, the hazard refers to the daily rate of death in our analyses. We refer to this technical meaning when using the term ‘hazard’ to discuss results from this model.

interval [CI] = 2.8–6.4] % for each increase in relative body mass by 0.1 SD (equivalent to ~100 g) above the mean (Figure 1). After then, the benefit of being relatively heavier for their age appeared to dissipate during the 1–1.5 years and was not clear in its direction and magnitude afterwards until the 4th year of life. Of note, there was no detectable association between infant body mass and maternal age in the present dataset (Figure 2, Supporting Information S5). We interpret the finding that infant body mass but not maternal age was linked to early life survival in the present hazards model as evidence for an independent contribution of being low body mass to early life survival.

3.2 | Is the duration of maternal care related to infant body mass?

In all, 32 mothers out of the 217 (15%) failed to reproduce again in the next year, and their infants were lower in relative infant body mass (mean \pm SEM = -0.29 ± 0.16) compared with those whose mothers reproduced again (0.07 ± 0.07 , $t_{46,24} = 2.09$, $p = 0.04$). After accounting for the potential influence of maternal age, primiparity, maternal rank, and birth timing on birth skipping, the probability of

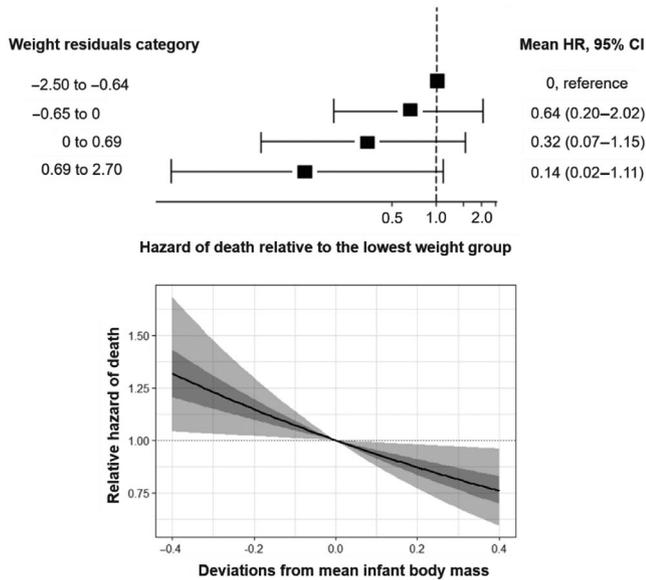


FIGURE 1 The relationship between infant body mass and survival during the 1st year of life ($N = 234$). Top: Hazard ratios (HRs) for each category of weight residuals, divided by their 1st quartile, mean, and 3rd quartile. HRs are in reference to the HR for the lowest weight residual category. Bottom: Post-estimation simulations (black line: mean, grey zone: 50% and 95% CI) from the hazards model (Table 1). The X-axis describes deviations of relative infant body mass (in SD) from the mean within age–sex class, and 0.1 SD corresponds to a deviation of ~100 g. The Y-axis describes the hazard of death relative to that of the mean infant body mass (horizontal dotted line). Values above 1 indicate a relative increase in the hazard. We used the R package SIMPH for simulations and visualization (Gandrud, 2015)

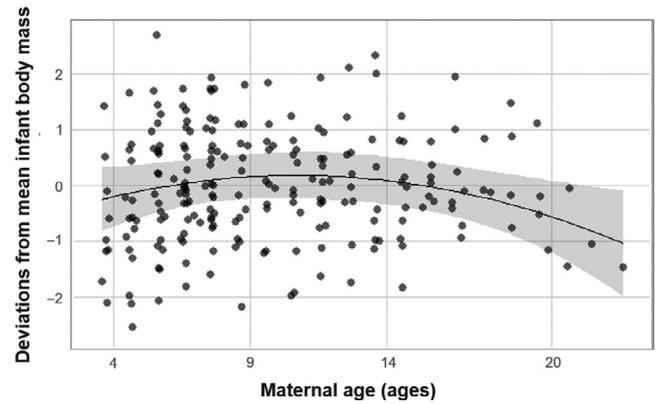


FIGURE 2 Relationship between infant body mass and maternal age, predicted by a model that controlled for other variables that may influence infant body mass in rhesus macaques (Supporting Information S5). The predicted line is overlaid with raw data points

TABLE 2 The relationship between infant body mass and birth skipping ($N = 217$). Estimates are bolded when their 95% CI's do not overlap with one (i.e., equivalent to zero for un-exponentiated coefficients)

	Coefficient estimate ^a		95% CI	
	e^β	SE	Lower	Upper
(Intercept)	0.12	0.61	0.03	0.34
Infant body mass	0.57	0.30	0.29	1.02
Maternal age (linear)	2.83	0.44	1.25	7.05
Maternal age (quadratic)	0.57	0.29	0.30	0.98
Primiparity	12.54	1.07	1.64	112.45
Maternal rank: middle	0.82	0.65	0.22	3.15
Maternal rank: low	0.62	0.65	0.16	2.26
Birth timing	2.55	0.26	1.63	4.69

^aSince coefficients are logit-transformed in logistic regression, we exponentiated the estimated coefficients. These transformed estimates are interpreted as proportionate change in the probability of event (here, birth skipping) compared with baseline (i.e., intercept coefficient) for a unit change in the covariate.

birth skipping was lower in average by 4.3% for an increase in relative infant body mass by 0.1 SD (Table 2) but the slight overlap of the 95% CI for the infant body mass variable with zero (i.e., equivalent to one for the exponentiated coefficient) indicated some uncertainty in the relationship between infant body mass and the risk that a mother skips next reproduction (Figure 3). As expected based on previous literature, the risk of birth skipping was higher for younger and older mothers, first-time mothers, and for mothers whose current offspring was born later during a birth season. We did not find evidence that infant body mass is related to maternal care as assessed by the duration of suckling, as the best-fitting GLM obtained through model selection did not retain the infant body mass variable (Supporting Information S6).

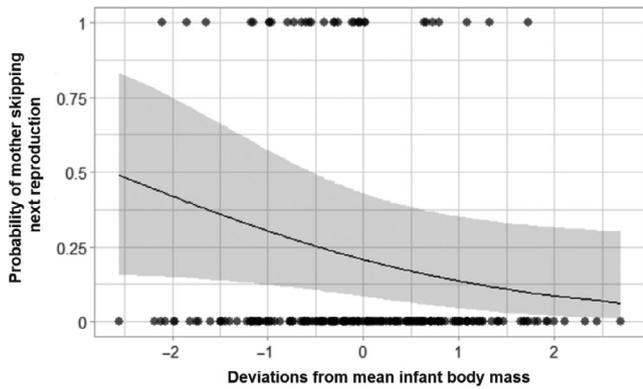


FIGURE 3 The predicted relationship between infant body mass and the probability of birth skipping ($N = 217$). Overlaid are raw data points (black circles), both for when birth skipping did not occur (y -axis at 0), and for when birth skipping occurred (y -axis at 1)

4 | DISCUSSION

Using the infant body mass data assessed prior to weaning, we found that lower body mass is associated with an increased risk of dying before maturation in free-ranging rhesus macaques, consistent with general findings from other large-bodied mammals (e.g. Clutton-Brock et al., 1992; Gaillard et al., 1997; Loison et al., 1999; Plard et al., 2015). The mortality risk due to being lighter in body mass was clearest in the 1st year of life and then gradually disappeared, with a less clear pattern between the 1.5th and 4th year of life. The link between infant body mass persisted after adjusting for other maternal effects on offspring mortality. It had been previously shown in rhesus macaques that offspring mortality is heightened for young and old mothers especially during the early life, but not necessarily for primiparous mothers (Blomquist, 2013; Nuñez et al., 2015). This observation, together with our finding that the present hazards model did not pick up maternal effect of age on offspring mortality, suggests that the maternal effect of age on offspring mortality may in part be mediated through low infant body mass in young or old mothers. Indeed, infant body mass was lower in young or old mothers in the current dataset (Supporting Information S4). Overall, these findings indicate the presence of an independent link between infant body mass and early life survival, while it remains a future task to learn the mechanism underlying this link and its potential role in mediating other environmental effects on early life survival.

When we further examined the duration of maternal care provided to offspring, we found some evidence that mothers rearing lighter offspring may be delayed in next reproduction due to the increased risk of birth skipping. The statistical evidence for this observation was unclear given the overlap of the 95% CI of the infant body mass with zero, suggesting some degree of confounding of the link between infant body mass and the risk of delayed reproduction in mother. The confound could have been due to factors influencing maternal capacity to shift the allocation of resources to next reproduction such as maternal age. However, given that the degree of

overlap with zero was only slight, we interpret the finding as suggesting a possibility that the duration of maternal care is adjusted according to the body mass of current offspring, in line with a view that the need for ensuring optimal growth and survival in offspring constrains maternal reproductive transition. While faster reproductive transition could be a reproductive advantage to a mother, it may only be so if offspring fitness is not jeopardized by shifting maternal allocation to the subsequent bout of reproduction (Altmann, 1983). Evidence from anthropoid primates suggests that offspring viability may indeed benefit from a longer interval to the next sibling's birth, such as in rhesus macaques, in which efforts to increase progeny production via shorter inter-birth intervals incur survival costs to the existing offspring (Lee et al., 2019). In such conditions, mothers could enhance reproductive success by improving offspring survival. This reproductive tactic is particularly relevant in primate life history where, due to the high uncertainty in juvenile recruitment, a primate mother would provide extensive parental care to ensure successful offspring recruitment at a given reproductive event (Altmann, 1998; Janson & van Schaik, 2002).

Despite the evidence that lighter offspring may be receiving more maternal care, the measure of maternal allocation used in the present study, week-age at the cessation of suckling, was not related to infant body mass. It thus remains unclear what forms of extra care the lighter offspring might have received during the extended maternal care with potential benefits in the offspring's chance of survival. Due to their long lifespans and highly differentiated social lives, maternal care in primates is often prolonged and expanded beyond basic direct physical care to include social support and learning opportunities (Altmann, 1980; Berman, 1986; Fairbanks & McGuire, 1988; Maestripieri, 2018; van Noordwijk, 2012; Silk et al., 2003). The extensive care provided by primate mothers is influenced by numerous factors including the presence of sibling (Silk, 1991). For example, among the rhesus macaques of Cayo Santiago, the amount of time in contact between mother and offspring abruptly decreases, and the frequency of maternal aggression towards yearlings increases, after sibling birth (Berman, 1992; Deviney, Berman, & Rasmussen, 2001). It is therefore possible that the relaxed mother–infant interactions experienced by the infants with lighter body mass, who may be delayed for sibling birth than the heavier infants, contributes to improve their growth or survival.

Although it is generally known that the ovarian cycle is suppressed during lactation based on the physiological constraint of lactation on reproduction (McNeilly, Tay, & Glasier, 1994), our finding suggests that allocation in current offspring (lactation) and future reproduction (resumption of ovarian cycle) might not have been strictly traded off. Suckling behaviours did not decline prior to the beginning of mating season (i.e. when mothers resume reproductive behaviours) but persisted even after the mothers became pregnant with their next offspring. Indeed, changes in serum stable isotope ratios show that captive rhesus macaques successfully conceive their next offspring during ongoing nutritive suckling (Reitsem et al., 2015). In humans, breastfeeding while pregnant

may not impose a significant risk to pregnancy (Cetin et al., 2014; López-Fernández, Barrios, Goberna-Tricas, & Gómez-Benito, 2017; Molitoris, 2019) especially if the current child is consuming other food (Molitoris, 2019). The duration of suckling may be better understood as a non-depreciable maternal care, allowing for a mother to allocate resources to multiple bouts of reproduction at the same time. Such a strategy could be particularly useful under the influence of reproductive synchrony where rhesus macaque females prioritize re-conception while their current infant is still young. But it remains unclear if this is an artefact of provisioning and to what extent the suckling has nutritional significance or is closer to 'comfort' nursing.

In conclusion, we showed that free-ranging rhesus macaques on Cayo Santiago who were relatively lower in body mass at infancy are less likely to survive until maturity. The positive association between infant body mass and early life survival is consistent with previous findings, which have been mostly based on large mammalian herbivores (Ronget et al., 2018). These studies have highlighted body mass during early life as key variable in determining how environmental factors that increase mortality risk, for example, climatic fluctuations of food availability or predatory risks, influence early life survival (Gaillard et al., 1997; Kjellander, Gaillard, & Hewison, 2006; Plard et al., 2015). The present study, based on a population where those factors are likely to vary less due to provisioning, demonstrates the persistent link between infant body mass and early life survival. It thus allows us a more direct investigation into factors such as maternal effects that affect offspring traits. One such factor suggested from this study is maternal age—infant body mass was lower for young or old mothers, who may be restricted in the resources that they can mobilize for reproduction (Dufour & Sautner, 2002; Hoffman et al., 2010). Future studies will benefit from testing the present study questions in wild settings where early life survival and maternal resource availability tend to be under stronger ecological constraints, and examining the mechanisms by which different predictors of infant and maternal conditions influence early life survival, for example by using path analysis (e.g. Plard et al., 2015). These efforts will in turn help better understand how variation in reproductive success arises in the females of monotocous iteroparous species such as long-lived mammals, who have evolved to prioritize improving offspring survival in the context of low reproductive rates.

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AUTHORS' CONTRIBUTIONS

D.S.L. and J.P.H. conceived the ideas; A.W., T.M.M. and C.D. provided data on body mass and behaviours; D.S.L. analysed the data; D.S.L. and J.P.H. led the writing of the manuscript. All authors provided feedback on the manuscript and gave final approval for submission.

DATA AVAILABILITY STATEMENT

Data used in the present study are deposited in the figshare data depository at <https://doi.org/10.6084/m9.figshare.12471764> (Lee, Mandalaywala, Dubuc, Widdig, & Higham, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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