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Infant survival is significantly impacted by dam- and management-related factors in zoo-managed *Eulemur* populations

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Abstract

Due to their potential impact on population growth, many studies have investigated factors affecting infant survival in mammal populations under human care. Here we used more than 30 years of Association of Zoos and Aquariums (AZA) studbook data and contraception data from the AZA Reproductive Management Center, along with logistic regression models, to investigate which factors affect infant survival in four *Eulemur* species managed as Species Survival Plans® in AZA. Across species, infant survival to 1 month ranged from 65% to 78%. Previous experience producing surviving offspring was positively correlated to infant survival in collared (*Eulemur collaris*), crowned (*Eulemur coronatus*), and mongoose (*Eulemur mongoz*) lemurs. Both dam age and previous use of contraception were negatively correlated to infant survival for collared lemurs, though our results suggest the latter may be confounded with other factors. Blue-eyed black lemurs (*Eulemur flavifrons*) were affected by birth location, suggesting differences in husbandry that may affect infant survival. These results can be used to assist in reproductive planning or to anticipate the likelihood of breeding success. Population managers may also be able to focus their reproductive planning on younger dams or those with previous experience to predict successful births. Future studies should seek to determine what aspects of previous dam success are most important to infant survival, investigate sire-related factors, and examine factors related to cause of death in infants that may lead to differential survival. Our hope is to present a framework that may be useful for investigating infant survival in other mammal species' breeding programs.

KEYWORDS

contraception, demography, ex situ management, maternal effects, neonatal mortality, reproduction

1 | INTRODUCTION

Modern zoos and aquaria strive for sustainable ex situ breeding programs to support education and conservation goals without removing individuals from wild sources. The Association of Zoos and Aquariums (AZA) has defined sustainability as having 90% gene diversity for 100 years or 10 generations (Ballou et al., 2010), with populations often requiring the addition of new founders to meet this goal. Since many populations cannot add new founders, managers must prioritize planned reproduction, an increase in holders, and global collaboration. To attain population sustainability without imports from external sources (wild populations or other ex situ programs, in the case of zoo populations), populations must produce enough surviving offspring to offset losses (Gotelli, 2008; Ranta et al., 2006), emphasizing the importance of consistent reproduction and offspring survival to maturity (Lees & Wilcken, 2009) for the health and viability of populations under human care.

We focus on infant survival in the genus *Eulemur*, which consists of 12 species of prosimians (Mittermeier et al., 2008), all endemic to Madagascar. While wild *Eulemurs* occupy nearly all of the forested area of Madagascar (Sato et al., 2015), individual species tend to be localized, such as collared lemurs (*Eulemur collaris*) in the southeast, mongoose lemurs (*Eulemur mongoz*) in the northwest, and blue-eyed black lemurs (*Eulemur flavifrons*) restricted to Sahamalaza-Iles Radama National Park (Mittermeier et al., 2008; Volampeno et al., 2015). Populations of all 12 *Eulemur* species have been maintained and have successfully reproduced in human care (Zehr et al., 2014); six are managed as one of the AZA's Species Survival Plan® (SSPs) (crowned lemur [*Eulemur coronatus*], collared lemur, blue-eyed black lemur, and mongoose lemur), or as an ex situ Program by the European Association of Zoos and Aquaria (EAZA; red-bellied lemur [*Eulemur rubriventer*], black lemur [*Eulemur macaco*]).

Our work focuses on understanding factors that may influence infant survival in the four *Eulemur* species managed as SSP programs. Despite stable or growing populations and decades of ex situ breeding (since approximately 1964), these species do not meet AZA's sustainability criteria. To ensure healthy and growing populations, the programs aim to better understand infant survival and its relationship to dam experience (Prosimian Taxon Advisory Group, 2019).

Though similar in many ways, our four focal *Eulemur* species have slight social and reproductive differences that could influence infant survival. Under human care, mongoose and blue-eyed black lemur females consistently produce one offspring per year (97% and 96% of litters, respectively; Zehr et al., 2014), whereas collared and crowned lemur females produce multiple offspring (generally twins, occasionally triplets) in 23% and 24% of litters, respectively (Zehr et al., 2014). In all four species, the dam carries the infant after birth (van Schaik & Kappeler, 1993), but in studies of wild lemurs, dams were the sole caregiver for crowned (Tecot et al., 2013) and blue-eyed black (Volampeno et al., 2011) lemur infants, whereas mongoose lemurs involved the sire (Curtis & Zaramody, 1998), and collared lemur grand-dams shared the responsibilities (Kesch, 2009). Despite these differences, the Prosimian Taxon Advisory Group (2019) suggests maintaining *Eulemurs* as pairs with their dependent offspring, though husbandry practices also differ slightly across AZA facilities. We anticipate potential differences in infant survival due to these observed biological, husbandry, and management differences, despite their close evolutionary history.

Infant survival in both in situ and ex situ populations can be influenced by several infant-, parent-, and environmental-related factors. Parental neglect, infection, and trauma are common causes of poor survival in both settings (Delaski et al., 2015; Lamglait, 2020; Mayor et al., 2006). In the wild, *Eulemur* infant birth weights, dam milk quality and age at first birth, and interbirth interval may vary based on environmental and social conditions (Wright, 1999). Fortunately, some factors affecting wild populations, such as group competition (Bayart & Simmen, 2005), seasonal fluctuations in food availability (Koyama et al., 2001; Parga & Lessnau, 2005; Tecot, 2010), and associated fluctuations in infant mortality (Overdorff et al., 1999), are less likely to affect *Eulemur* populations under human care; lemur dams under human care tend to begin breeding at a younger age, have shorter interbirth intervals, and produce heavier infants compared to their wild counterparts (Wright, 1999). As such, our work focuses on biological and experiential factors (e.g. age, parity) related to the infants and their parents instead. Understanding these factors could be beneficial in helping managers prepare for likely outcomes or plan additional steps to ensure infant survival.

Research Highlights

- *Eulemur* dam age, parity, contraception history, and location are associated with infant survival.
- Managers can use these findings to predict success of dams in their care and use these methods to analyze factors in other species.

Previous lemur studies have highlighted key infant-related factors that may affect infant survival. Infant survival was significantly lower among inbred brown lemurs (*Eulemur fulvus spp*.) and black lemurs under human care (Rails & Ballou, 1982), and Perry et al. (1992) noted a 52% higher mortality rate in mongoose lemur infants of dams born under human care compared to dams born in the wild. No significant relationship has been found between infant sex and infant survival in investigated *Eulemur* species, including collared, mongoose, red brown (*Eulemur rufus*), and black lemurs (Perry et al., 1992; Watson et al., 1996). The impact of litter size varies across lemur species; increasing litter size in zoo-managed black-and-white ruffed lemurs (*Varecia variegata*; Schwitzer & Kaumanns, 2009) increased infant survival percentage, but Tidière et al. (2018) found that black-and-white ruffed and red ruffed (*Varecia rubra*) lemur infant survival was negatively influenced by litter size, and Debyser (1995) suggested no impact of litter size on prosimian juvenile survival.

Newborn primates are altricial (i.e., unable to feed or move independently) and parental care in these species can also impact infant survival, with sires and dams appearing to affect infant survival differently. The impact sires have on infant survival has not been studied in depth enough to be quantified, particularly in lemurs, although differences in paternal care across nonhuman primates suggest potential benefits and improved infant survival (Huck & Fernandez-Duque, 2013; Smuts & Gubernick, 2017). However, dam parity (i.e., experience) has been associated with infant survival in some prosimian species. Infant survival was significantly lower for primiparous dams in *Galago* species (Izard & Simons, 1986), and was 63.4% and 42.9% for multiparous and primiparous black-and-white ruffed lemur dams, respectively (Shideler & Lindburg, 1982). Infant survival was also higher for multiparous mongoose lemur dams (77.3%) than primiparous dams (50%), though this was not considered significant, potentially due to small sample size and interactions with confounding factors (Perry et al., 1992).

When assessing the impact of dams on infant survival, linear and quadratic age are often considered alongside parity as potential factors. Linear age implies a directional effect, with older dams showing increased or decreased infant survival. On the other hand, quadratic age could indicate reproductive senescence, suggesting a "prime" reproductive age around which infant survival may decrease due to factors like lack of dam experience (before prime age) or a decline in milk quality and quantity (after prime age; Tidière et al., 2018); this may suggest differing management strategies to promote infant survival around that prime age. Kappeler et al. (2022) found evidence for reproductive senescence in wild red-fronted lemurs (*Eulemur rufifrons*) and zoo-housed red lemurs, and Tidière et al. (2018) further demonstrated that infant survival of red-ruffed and black-and-white ruffed lemurs initially increased with dam age, then began to decrease as the dam approached reproductive senescence. In some primate taxa, increased dam age was positively associated with infant mortality (de Visser et al., 2022) or the likelihood of stillbirths (Saiyed et al., 2018), while others showed reduced infant survival for both the youngest and oldest dams (Campos et al., 2022). Given the conflicting results in previous studies regarding the relationships infant survival has with dam age and parity, factors that tend to be negatively correlated with each other, it is important to consider both linear and quadratic age.

Though many studies of infant survival in nonhuman mammals have focused on dam or infant biology, female contraception, another dam-related factor, can also affect infant survival in ex situ animal populations (Asa & Moresco, 2019). Zoos often use contraception to (1) manage breeding due to space limitations, (2) preserve genetic diversity of the population, and (3) maintain nonbreeding animals in social groups that benefit their welfare (Asa & Porton, 2010; Porton, 2005). Ensuring the long-term reproductive health of the individuals in these populations requires safe and reversible contraception with minimal long-term impact on fertility (Kirkpatrick & Turner, 1991). Though contraception offers potential benefits, relatively few studies have analyzed its impact on future offspring survival. Some primate studies link previous contraceptive use with increased stillbirths (Cappelletti et al., 2015; McDonald et al., 2020; Wood et al., 2001). Terranova and Coffman (1997) also found a positive association between increased weight and female contraception in blue-eyed black and crowned lemurs, and adult female *Eulemurs* under human care have historically experienced obesity, which has been found to negatively affect reproduction in multiple species (Hearn et al., 1996; Pereira & Pond, 1995; Schaaf & Stuart, 1983). The potential links between contraception, obesity, and reproductive concerns may suggest decreased infant survival for previously contracepted dams, though further evaluation in additional species is needed.

Animal managers seek to enhance the viability of *Eulemur* populations under their care by optimizing infant survival. The first-year mortality rate, which ranges from 22% to 42% for the four species included in our work (Becker & Ferrie, 2020; Ferrie & Schoffner, 2021; Hoppe & Ferrie, 2019; Sears & Ferrie, 2022), potentially inhibits population growth significantly. This paper aims to illuminate the factors available from retrospective population metrics that are associated with infant survival, providing guidance to lemur population managers on supporting population growth, and to provide a framework for analyzing infant survival, population characteristics, and husbandry records. Several diverse factors may affect infant survival for *Eulemur* species, with effects likely differing across species. Based on previous findings in *Eulemurs* and other mammals, we anticipate notable impacts of dam experience, contraception history, inbreeding levels, and parent origin (wild or ex situ birth) on infant survival.

2 | METHODS

2.1 | Data collection and predictor variables

We studied infant survival in four *Eulemur* species: mongoose lemur, crowned lemur, blue-eyed black lemur, and collared lemur. We collected data in the fall of 2020, using information available in their respective studbooks in ZIMS for Studbooks (Becker, 2020; Hoppe, 2019; Schoffner, 2020; Sears, 2019). We collected data on all individuals with known birth dates at AZA facilities after the start of the species' AZA breeding program (crowned—1979, blue-eyed black—1986, collared and mongoose—1964).

Data extracted from the studbooks included infant birth and death dates and locations, sex, parent studbook numbers, transfers between facilities, and any notes provided. While we believed rearing method (i.e., parent- or hand-reared) could affect infant survival, all individuals with information available were parent-reared, so the impact of management intervention on infant survival was not considered. We also obtained individual inbreeding coefficients calculated by PMx 1.6.2.20200110 (Ballou et al., 2020) and contraception data from the AZA Reproductive Management Center (AZA RMC/EAZA RMG, 2021).

From these data, we established several biologically important variables predicted to affect infant survival based on the literature. Some factors were extracted directly from the studbook database (e.g. birth year), whereas others needed to be calculated or mined from the data (e.g. parent age, parental parity). We defined primiparous parents as those with no previous experience producing offspring, whereas multiparous had previous experience, regardless of previous infant survival. We also included quadratic age (i.e., age-squared) to investigate potential reproductive senescence. Factors predicted to affect infant survival were separated into generalized factors used in our models (e.g. parity or contraception; Table 1) and more specific factors used in post hoc analyses of model-significant factors (e.g. number of previous offspring or time since contraception

TABLE 1 List of variables used in the initial global model (i.e., model including all variables) and subsequent global models for each species, before removal of collinear variables and those leading to singular fit.

Variable	Variable type	Description
SurvivalM	Binary— Yes/No	Infant did/did not survive to at least 30 days old—response variable
SurvivalD	Binary—Yes/No	Infant did/did not survive beyond its first day of life—response variable
Species	Categorical	Infant species
BirthYear	Numerical	Year of birth of the infant
BirthLocCat	Binary—Duke/Other	Location of birth of the infant, divided into DUKE PRIM or other facilities
Sex[a]	Binary—Male/Female	Infant sex
Twin	Binary—Yes/No	Infant considered a twin if born within 3 days of its maternal sibling
DamPar	Binary—Prim/Mult	Dam did/did not have previous experience producing offspring (i.e., primiparous or multiparous) regardless of infant survival
SirePar	Binary—Prim/Mult	Sire did/did not have previous experience producing offspring (i.e., primiparous or multiparous) regardless of infant survival
DamYear[b]	Numerical	Age of the dam (in years) on the birth date of the infant
DamYearSq[b]	Numerical	Age-squared of the dam (in years) on the birth date of the infant
SireYear[c]	Numerical	Age of the sire (in years) on the birth date of the infant
SireYearSq[c]	Numerical	Age-squared of the sire (in years) on the birth date of the infant
GenRemove[d]	Numerical	Number of generations removed from the wild, determined by following dam lineage backward and counting antecedents until the most recent wild-born female
DamYoung[d]	Binary—Yes/No	Dam did/did not have experience living at the same facility as a younger full- or maternal half-sibling[e] for the first 6 months of its life before giving birth herself
SireYoung[d]	Binary—Yes/No	Sire did/did not have experience living at the same facility as a younger full- or maternal half-sibling[e] for the first 6 months of its life before the birth of his first offspring
DamCont	Binary—Yes/No	Dam was/was not ever contracepted before the birth of the infant
Inbreed	Numerical	Inbreeding coefficient of the infant, calculated from PMx 1.6.2.20200110 (Ballou et al., 2020)

Note: Italicized factors were removed from the models for the reasons stated below.

[a]Sex was removed due to (1) the similar survival rate across sexes and (2) the increase in sample size for nonsurviving individuals when sex was excluded.

[b]These factors are reported in years for ease of interpretation, but are rounded to the nearest day through their decimals.

[c]These factors were removed to increase the sample size due to the amount of missing data.

[d]These variables were eliminated due to high correlation with at least one other variable deemed to have more potential importance to the model.

[e]Siblings were only considered if they were born within 7 years of each other. Approximately 85% of individuals had transferred to a facility separate from their dam by this age; since there is likely a reason for this separation, it is likely that those still at the same facility as their dam would also have been separated for the same reason.

was ceased; Table 2). This separation aims to prevent model oversaturation and increase sample sizes where only broader data were available. As this research was not performed on humans/animals, an ethics statement is not applicable to this work.

2.2 | Summary statistics

We focused on two binary infant survival measures, survival beyond 30 days and survival beyond 1 day. Surviving infants were those that lived beyond their first day or first 30 days, and others were classified as nonsurviving; stillborn infants and those that died shortly after birth were included as nonsurviving infants for the 1-day survival metric. Survival to 1 month (commonly 28 or 30 days) is a standard threshold for primate infant survival research (Anderson & Dennis, 2018; Fuller et al., 2014; Nuss & Warneke, 2010; Zehr et al., 2014), potentially offering a solid overview of factors affecting infant survival; 1-day survival may relate more to stillbirth trends of health-related infant deaths. We determined overall infant survival rates as percentages of individuals surviving beyond 1 day and 30 days, and used this approach to compare infant survival rates among categorical predictors (e.g., percent survival of twins vs. singletons; Table 3). For numerical predictors, we calculated averages and standard deviations from values for survivors and nonsurvivors (Table 4). For our post hoc analyses, we used the stats package in R 4.0.3 (R Core Team, 2020) to assess infant survival differences within categorical variables (Chi-Square Tests of Independence; Fisher, 1922; Pearson, 1900) and for numerical variables (Mann–Whitney U test; Mann & Whitney, 1947).

TABLE 2 List of variables used in post hoc analyses to gain more specific insight into factors deemed important through model selection.

Variable	Variable type	Description
DamPrevCount	Numerical	Number of previous reproductive events of the dam, regardless of infant survival
DamPrevCountM	Numerical	Number of previous reproductive events of the dam that produced at least one infant that survived at least 30 days
LastBirth	Numerical	Interbirth interval, or number of years between the birth date of the infant and the date of the next most recent birth, regardless of infant survival
SibSurvive	Numerical	Percent of previous reproductive events of the dam that produced at least one infant that survived 30 days
LastSurvive	Binary—Yes/No	At least one infant from the most recent reproductive event of the dam did/did not survive 30 days
DamFirst	Numerical	Age of the dam (in years[a]) on date of her first reproductive event, regardless of infant survival
SireFirst	Numerical	Age of the sire (in years[a]) on date of birth of his first offspring, regardless of infant survival
DamTotalCont	Numerical	Amount of time dam was contracepted (in years[a]) before the birth of the infant
TimeSinceStop	Numerical	Amount of time since the most recent bout of contraception was ceased (in years[a]) before the birth of the infant
FirstOff	Binary—Yes/No	Infant was/was not the first infant born after the dam was removed from contraception
MostRecentCont	Categorical—None/melengestrol acetate/Depo-Provera (medroxyprogesterone acetate)/Suprelorin (deslorelin acetate)	Type of contraception dam was most recently on before birth of the infant

[a]These factors are reported in years for ease of interpretation, but are rounded to the nearest day through their decimals.

2.3 | Model selection

Our initial aim was to use a mixed effects logistic regression model, with individual dam and sire as random effects. However, these led to singular fits (i.e., all samples in the category share the same response, causing variance for the effect to equal zero), so we proceeded with a fixed effects logistic regression model including biologically significant predictors (Table 1) for initial model selection. Sex-based survival rate differences were insignificant (Table 3; $\chi^2 = 0.05$, $p = .8199$), consistent with previous *Eulemur* studies (Perry et al., 1992; Watson et al., 1996), so we removed infant sex from our model to increase the sample size of nonsurviving individuals by approximately 20%, as infants with unknown sex ($N = 31$) could not be included. We also removed the age factors for sires to include the 105 infants missing sire-related data. Infants in this study were born at 32 facilities, with 56% of infants born at the Duke Lemur Center ($N = 286$) and the next most prevalent birth location only representing 6% of births, so we created a binary birth location factor distinguishing Duke Lemur Center from other facilities. All models used infant survival as the binomial response variable, with infants either surviving (1) or not surviving (0) their first day or first month. We assessed factor collinearity in R 4.0.3 (R Core Team, 2020) using the vif() program from the car package (v3.0-10; Fox & Weisberg, 2019) to produce variance inflation factors, and removed variables identified as collinear (VIF > 5; Stine & Stine, 1995). Birth year and generations removed from the wild were collinear, so the latter was removed from the models; dam and sire experience with their younger siblings were collinear with most other factors, so they were also both removed. Due to significant collinearity, we could not create a model for 1-day survival of collared lemurs with more than one factor, so this model was not run. Attempts to include interaction effects between parity and age and between birth year and birth location did not result in model convergence, leading to their removal as well.

For model selection, we first eliminated individuals with missing or unknown values for the remaining predictors ($N = 102$ removed), a requirement for the model selection program used. Using R 4.0.3 (R Core Team, 2020) and the dredge() program in the MuMIn package (v 1.43.17; Barton, 2020), we created an average model from the most parsimonious models; models included in the average had an AICc difference (ΔAICc) <2 when compared to the most parsimonious model (see Supporting Information S1 for models included in the individual and average models). We used AICc instead of AIC due to the relatively small sample sizes, setting ΔAICc threshold to two as it is a standard in estimating parsimony (Burnham & Anderson, 2002). This process was first completed at the genus level with data from all

TABLE 3 Number of infants in each category and infant survival rate for the initial categorical variables listed in Table 1; *N* values for variables that do not add to the total for the species indicate some individuals were missing data for that variable.

		Collared lemur *Eulemur collaris*			Crowned lemur *Eulemur coronatus*			Blue-eyed black lemur *Eulemur flavifrons*			Mongoose lemur *Eulemur mongoz*		
		N	% survived day	% survived month	*N*	% survived day	% survived month	*N*	% survived day	% survived month	*N*	% survived day	% survived month
Species Overall Survival		108	89	78	113	83	66	94	76	65	199	88	76
BirthLocCat	Duke	62	85	76	68	85	65	71	85	76	85	86	74
	Other	46	93	80	45	80	69	23	48	30	114	89	78
Sex	Male	53	87	81	66	89	71	46	80	72	100	92	79
	Female	48	98	85	37	86	73	43	79	65	90	89	81
Twin	Yes	36	89	69	51	84	61	10	70	60	18	89	61
	No	72	89	82	62	82	71	84	76	65	181	88	78
DamPar	Prim	30	87	77	23	65	52	15	60	47	42	81	60
	Mult	77	91	79	90	88	70	74	78	69	153	90	81
SirePar	Prim	21	81	71	23	87	78	14	71	64	36	78	61
	Mult	77	90	78	88	84	65	78	76	65	155	90	79
DamYoung	Yes	39	90	82	52	81	65	35	71	60	73	88	75
	No	54	98	87	54	91	70	24	67	63	81	86	75
SireYoung	Yes	49	94	84	41	90	71	48	77	75	67	87	73
	No	24	88	75	52	77	69	23	61	48	78	86	77
DamCont	Yes	23	83	63	20	80	70	36	64	50	44	82	75
	No	83	90	82	93	84	66	58	83	74	152	89	76

Note: Variables in italics were removed from the model (see Table 1).

four species to determine if we should proceed using all four species combined or treated separately. Since infant mortality differed significantly by species (Table 5), we repeated the process for each species independently. We calculated descriptive survival statistics to gain insight on additional factors (Table 2) related to the predictors deemed significant ($p \le .05$) for each species in the average model. We used the full data set in these calculations, including individuals that had been removed from model selection due to missing data for other variables. Given the similarity in model results and post hoc analysis results between 1-day and 1-month survival, we only report results from post hoc analyses of 1-month survival except where otherwise specified.

3 | RESULTS

We calculated summary and descriptive statistics using our full data set of 514 individuals (collared lemur—*N* = 108, crowned lemur—*N* = 113, blue-eyed black lemur—*N* = 94, mongoose lemur—*N* = 199). Among these, 412 (80%) had complete data and were used in model selection (collared lemur—*N* = 84, crowned lemur—*N* = 113, blue-eyed black lemur—*N* = 59, mongoose lemur—*N* = 156).

Across all four species, 72% of infants survived to 1 month. Of those that did not survive the month, 87% died within 5 days and 55% did not survive beyond a day (15% of all infants); all nonsurviving collared lemur infants died within 5 days (Figure 1). Percent infant survival (for categorical variables) and average values for surviving and nonsurviving infants (for numerical variables) are listed in Tables 3 and 4, respectively. At the genus level, 30-day infant survival rate differed significantly across species, as well as by previous dam experience, dam contraception history, and birth year. All four variables had a relative importance of 1, indicating consistent impacts on infant survival (Table 5). Primiparous dams and previously contracepted dams had significantly lower infant survival rates, and infant survival rates tended to improve overall as birth years progressed (i.e., approached present day). Previous contraception use in the dam did not significantly affect infant survival beyond the first day. Overall infant survival rates to 1 month for each species are shown in Figure 2.

3.1 | Collared lemur (*E. collaris*)

Seven predictors were included in the most parsimonious models, with four demonstrating significant impacts on infant survival to

TABLE 4 Average value (± standard deviation) for surviving and nonsurviving infants for each of the initial numerical variables listed in Table 1.

			Collared lemur *Eulemur collaris*	Crowned lemur *Eulemur coronatus*	Blue-eyed black lemur *Eulemur flavifrons*	Mongoose lemur *Eulemur mongoz*
DamYear	Day	Survived	6.74 (4.34)	7.68 (3.95)	6.42 (4.01)	7.67 (4.31)
		Did not survive	12.69 (7.06)	8.10 (5.36)	8.55 (4.33)	8.45 (4.72)
	Month	Survived	6.25 (4.01)	7.89 (4.06)	6.37 (4.19)	7.89 (4.33)
		Did not survive	11.76 (5.81)	7.49 (4.48)	8.15 (4.04)	7.4 (4.48)
SireYear	Day	Survived	12.23 (7.06)	8.15 (4.31)	9.49 (5.79)	10.26 (5.33)
		Did not survive	9.92 (7.12)	6.48 (3.32)	9.28 (5.90)	8.33 (5.65)
	Month	Survived	12.57 (7.28)	7.77 (4.26)	9.73 (5.97)	10.90 (5.36)
		Did not survive	10.26 (5.87)	8.08 (4.10)	8.84 (5.47)	8.49 (5.68)
GenRemove	Day	Survived	3.40 (1.71)	3.78 (1.43)	1.91 (0.99)	2.50 (1.31)
		Did not survive	2.65 (1.77)	3.95 (1.91)	2.08 (0.84)	2.75 (1.29)
	Month	Survived	3.48 (1.68)	3.91 (1.53)	1.95 (0.97)	2.49 (1.31)
		Did not survive	2.58 (1.74)	3.63 (1.50)	1.97 (0.92)	2.67 (1.32)
Inbreed	Day	Survived	0.144 (0.096)	0.159 (0.131)	0.069 (0.068)	0.028 (0.044)
		Did not survive	0.108 (0.119)	0.171 (0.118)	0.072 (0.062)	0.056 (0.086)
	Month	Survived	0.148 (0.095)	0.171 (0.122)	0.070 (0.069)	0.027 (0.044)
		Did not survive	0.114 (0.108)	0.140 (0.140)	0.070 (0.061)	0.045 (0.069)
BirthYear	Day	Survived	1995 (12.9)	2000 (11.8)	2002 (10.5)	1996 (14.6)
		Did not survive	1986 (19.5)	2002 (13.4)	2004 (8.5)	1998 (14.2)
	Month	Survived	1996 (12.9)	2001 (12.3)	2002 (10.7)	1996 (14.8)
		Did not survive	1989 (16.4)	1999 (11.5)	2003 (8.8)	1997 (13.7)

Note: Variables in italics were removed from the model due to high correlation (see Table 1).

1 month (Table 6). The likelihood of infant survival significantly increased with later birth years. However, infant survival decreased as the dam aged (Table 6), and post hoc analyses suggested that successful dams were younger (3.16 ± 2.62 years) at age of first reproduction than unsuccessful dams (9.90 ± 6.61 years; U = 1038, $p < .0001$). The quadratic age factor of the dam did not appear in any of the top models.

The likelihood of survival to 1 month significantly increased if the infant had an experienced dam (Table 6). Infant survival was positively affected by the number of previous offspring that survived (U = 719.5, $p = .0287$), but not by the number of offspring previously produced when nonsurviving infants were included (U = 965.5, $p = .7520$). Among dams with previous experience, those whose most recent infant survived were significantly more likely to produce another surviving infant ($\chi^2 = 16.58$, $p < .0001$), with an 89% infant survival rate for dams whose most recent infant survived and only a 36% infant survival rate for those whose most recent infant did not survive. Additionally, the percent of siblings that survived did not have a significant impact on infant survival (U = 149.5, $p = .0524$), nor did the interbirth interval (U = 529, $p = .6111$).

Infants whose dams had been previously contracepted had a lower likelihood of survival to 1 month. Among infants of previously contracepted dams ($N = 23$), the duration of previous contraception had no impact on infant survival (U = 50, $p = .3917$), nor did the time passed since contraception was stopped (U = 51, $p = .1292$). There was also no significant difference in infant survival between the first offspring produced after contraception ended (66% survival) and subsequent postcontraception offspring (33% survival; $\chi^2 = 1.1269$, $p = .2884$), though this could be attributed to the small sample size ($N = 12$ and $N = 6$ for first postcontraception offspring and other postcontraception offspring, respectively). Survival rates for infants of dams contracepted with Depo-Provera and melengestrol acetate were identical (62.5%), suggesting type of contraception does not affect infant survival in this species. Dams that were previously contracepted tended to be older on average at the date of birth (9.30 years across previously contracepted dams; 7.69 years for surviving infants, 12.95 years for nonsurviving infants) than noncontracepted dams (6.52 years across noncontracepted dams; 5.93 years for surviving infants, 10.23 years for nonsurviving

TABLE 5 Results of averaged global models predicting the likelihood of infant survival to (A) 1 month and (B) beyond 1 day for the four species of *Eulemur*.

(A)							
All species—*N* = 514		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 412**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	−45.370	23.270	(−91.119, 0.372)	.0519
Species	*Eulemur collaris*	1	100			Reference	
	Eulemur coronatus			−1.203	0.375	(−1.941, −0.466)	.0014
	Eulemur flavifrons			−1.485	0.444	(−2.358, −0.612)	.0009
	Eulemur mongoz			−0.817	0.381	(−1.565, −0.069)	.0324
BirthLocCat	Duke	0.16	0			Reference	
	Other			−0.038	0.141	(−0.315, 0.239)	.7887
Twin	No	0.67	0			Reference	
	Yes			−0.322	0.322	(−0.954, 0.311)	.3190
DamPar	Mult	1	100			Reference	
	Prim			−1.204	0.298	(−1.790, −0.619)	.0001
SirePar	Mult	0.26	0			Reference	
	Prim			0.088	0.227	(−0.357, 0.533)	.6976
DamCont	No	1	80			Reference	
	Yes			−0.618	0.294	(−1.197, −0.039)	.0364
BirthYear		1	90	0.024	0.012	(0.001, 0.047)	.0399
DamYear		0.72	70	−0.048	0.039	(−0.124, 0.028)	.2194
DamYearSq		0.28	30	−0.001	0.001	(−0.004, 0.002)	.5850
Inbreed		0.07	0	0.050	0.415	(−0.765, 0.864)	.9052
(B)							
All Species—*N* = 514		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 412**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	−1.839	17.274	(−35.750, 32.071)	.9153
Species	*E. collaris*	1	100			Reference	
	E. coronatus			−1.122	0.497	(−2.099, −0.145)	.0244
	E. flavifrons			−1.872	0.530	(−2.913, −0.831)	.0004
	E. mongoz			−0.760	0.487	(−1.718, 0.197)	.1195
BirthLocCat	Duke	0.06	0			Reference	
	Other			−0.010	0.080	(−0.167, 0.148)	.9053
Twin	No	0.12	0			Reference	
	Yes			0.027	0.143	(−0.255, 0.308)	.8533
DamPar	Mult	1	100			Reference	
	Prim			−1.350	0.346	(−2.030, −0.670)	.0001
SirePar	Mult	0.13	0			Reference	
	Prim			0.039	0.176	(−0.307, 0.384)	.8265
DamCont	No	0.53	0			Reference	
	Yes			−0.283	0.366	(−1.002, 0.436)	.4400
BirthYear		0.20	0	0.003	0.009	(−0.014, 0.020)	.7371

(Continues)

TABLE 5 (Continued)

(B)						
All Species—*N* = 514	**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 412**			
Predictors	**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
DamYear	0.88	76.9	−0.103	0.066	(−0.232, 0.026)	.1185
DamYearSq	0.23	7.7	0.000	0.003	(−0.005, 0.005)	.9204
Inbreed	0.05	0	−0.043	0.422	(−0.872, 0.786)	.9195

Note: Only predictors that appeared in the most parsimonious models (ΔAICc < 2) are shown; the predictor was significant for the percent of the most parsimonious models listed (see Supporting Information S1 for further detail). Bolded predictors significantly affected infant survival, based on the *p* value from the averaged model.

Abbreviation: CI, confidence interval.

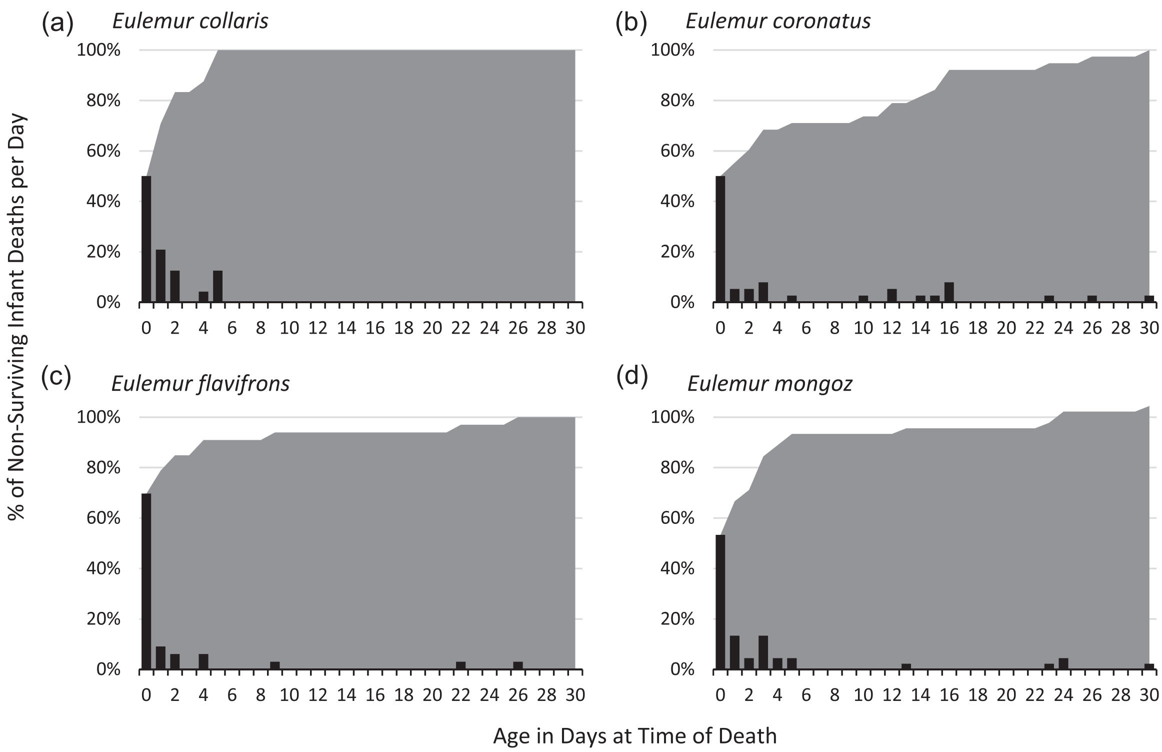

FIGURE 1 Number of days (bars) lived for infants that did not survive the first month and cumulative percent of first-month deaths by day (shaded area) for (a) collared lemur, (b) crowned lemur, (c) blue-eyed black lemur, and (d) mongoose lemur.

infants); previously contracepted dams also tended to begin reproducing at a later age (6.11 years) than noncontracepted dams (3.69 years).

3.2 | Crowned lemur (*E. coronatus*)

The most parsimonious models for crowned lemurs included seven predictors, with both dam and sire parity affecting infant survival to 1 month (Table 7A) and dam parity affecting infant survival beyond the first day (Table 7B). Primiparous sires had higher infant survival rates than their multiparous counterparts; primiparous sires tend to be younger than multiparous sires on average (6.36 ± 3.78 years compared to 8.22 ± 5.74 years), though there is no significant difference in survival by age at which the sire first reproduced ($U = 846$, $p = .5961$). Conversely, primiparous dams had significantly lower infant survival rates than multiparous dams. Infant survival was slightly lower when the infant was the first born to the dam-sire pair (60%) compared to infants that had older full siblings (68%).

The total number of previous offspring of the dam was significantly positively correlated with survival to 1 month ($U = 1101$, $p = .0473$), whereas the number of previous surviving

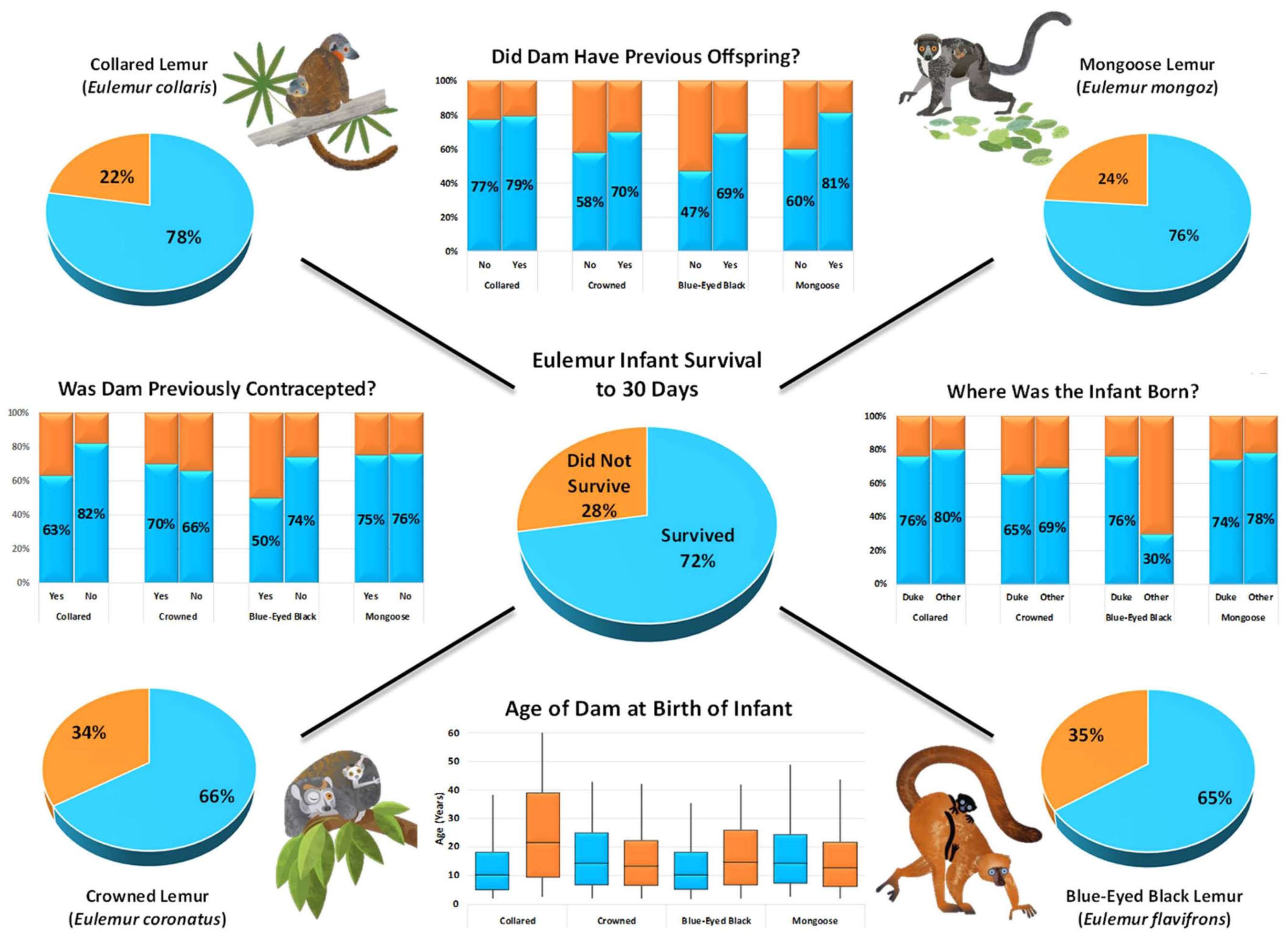

FIGURE 2 Summary of survival rates for four species of *Eulemur*, with factors that demonstrate a significant impact on infant survival. Pie charts show overall survival and column charts show the percent survival for each category. Chart of dam age at infant birth represents the median and quartiles for each group. Blue represents surviving infants and orange represents nonsurviving infants in all charts.

offspring of the dam was not significant (U = 1108.5, p = .0509), though this factor was significant in 1-day survival (U = 523, p = .0039). Crowned lemur dams whose most recent infant survived had a higher infant survival rate (74%) than dams whose most recent infant did not survive (57%), though not significantly (χ^2 = 1.432, p = .2315). Further, neither the percent of previous offspring that survived (U = 818.5, p = .7795) nor the interbirth interval (U = 529, p = .6111) had an impact on infant survival.

3.3 | Blue-eyed black lemur (*E. flavifrons*)

Six factors were included in the most parsimonious models for blue-eyed black lemur, with infants born at Duke Lemur Center demonstrating a significantly higher likelihood of survival beyond 1 day and to 1 month compared to those born elsewhere (Table 8A and 8B). Though birth location was not collinear with other factors, only 20 of the 71 (28%) infants born at the Duke Lemur Center had previously contracepted dams (13 of which had the same dam), whereas 16 of the 21 (76%) infants born elsewhere had contracepted dams. Duke also had younger dams on average (6.46 years) than other facilities (8.25 years), with a slightly lower age at first reproduction (3.23 years compared to 4.32 years), and had a higher percentage of infants born to multiparous dams (92.4%) than other facilities (73.9%). While these were also not collinear with birth location, it is possible these factors are confounded.

3.4 | Mongoose lemur (*E. mongoz*)

The most parsimonious models for mongoose lemurs contained six factors, and mongoose lemur infants with experienced dams were significantly more likely to survive to 1 month than those with inexperienced dams (Table 9A). The number of previous surviving offspring was positively correlated with infant survival (U = 2827, p = .0274), whereas the total number of previous offspring was not

TABLE 6 Results of average models predicting the likelihood of infant survival for collared lemurs (*Eulemur collaris*).

E. collaris—*N* = 108		Parsimonious models (ΔAICc < 2)		Averaged model—*N* = 84			
Predictors		Relative importance	Percent significant	Estimate	Standard error	95% CI	p Value
(Intercept)		N/A	N/A	−326.641	145.140	(−615.178, −38.104)	.0265
BirthLocCat	Duke	0.32	0	Reference			
	Other			−0.447	0.910	(−2.244, 1.350)	.6261
DamPar	Mult	1	100	Reference			
	Prim			−2.403	0.992	(−4.378, −0.429)	.0171
SirePar	Mult	0.21	0	Reference			
	Prim			−0.260	0.708	(−1.658, 1.138)	.7158
DamCont	No	1	100	Reference			
	Yes			−2.269	0.926	(−4.111, −0.427)	.0158
BirthYear		1	100	0.167	0.074	(0.021, 0.314)	.0249
DamYear		1	100	−0.427	0.133	(−0.693, −0.162)	.0016
Inbreed		0.27	0	1.236	3.270	(−5.230, 7.701)	.7080

Note: Only predictors that appeared in the most parsimonious models (ΔAICc < 2) are shown; the predictor was significant for the percent of the most parsimonious models listed (see Supporting Information S1 for further detail). Bolded predictors significantly affected infant survival, based on the *p* value from the averaged model.

Abbreviation: CI, confidence interval.

(though it did trend toward having a significant impact; U = 2999, $p = .0923$). Infant survival rates were higher for dams whose most recent infant survived (84%) compared to those whose did not (70%), but this difference was not significant ($\chi^2 = 2.137$, $p = .1438$); percent of siblings that survived (U = 1309, $p = .1416$) and interbirth interval (U = 1936, $p = .5221$) also did not significantly impact infant survival rates.

4 | DISCUSSION

We reviewed data for individuals of four *Eulemur* species in AZA-accredited zoological facilities and used logistic regression models to identify factors that may affect infant survival. We investigated factors including twin status, dam and sire experience, dam age, dam contraceptive history, and birth year and location. Though the four *Eulemur* species analyzed in this study differ in factors affecting infant survival, our work highlights the consistent role of dam- and management-related factors in predicting infant survival, offering valuable insights for husbandry and management practices.

Our initial genus-level analysis revealed significant effects of species, dam parity, previous contraception, and birth year on infant survival. Differences across species are understandable given their distinct life histories (e.g., Zehr et al., 2014) and variations in facility goals and experience levels. While dam parity was significantly related to infant survival in three of the four species, genus-level results do not seem to reveal the full picture in our study, as evident in species-specific differences across other variables. Previous contraception and birth year were both only significant for collared lemurs, suggesting this species largely drove the inclusion of these factors in the genus-level analyses. Additionally, the inability to obtain results for 1-day infant survival for collared lemurs due to collinearity suggests either multiple factors were equally impactful on infant survival or none of the included factors were. These findings illustrate the potential benefits of examining datasets at both the genus and species level; genus-level analyses offer a larger sample size but more generalized results, whereas species-level analyses may provide higher resolution with smaller sample sizes.

In all four species, primiparous dams had a lower likelihood of survival of their first infant, a significant difference in three of them (collared, crowned, and mongoose lemurs), which suggests a need for caretakers to provide an increased focus on pregnant primiparous females to help decrease infant mortality in this group. In collared and mongoose lemurs, previous success raising offspring beyond 30 days positively correlated with infant survival, whereas simply birthing an offspring that did not live to 30 days did not correlate with future success. This suggests that experience raising offspring, as opposed to simply experiencing pregnancy and parturition, may improve the likelihood of future infants surviving. Studies of other primates have noted similar patterns; Perry et al. (1992) noted first-day infant mortality (including stillbirths) of primiparous mongoose lemur dams was more than double that of their multiparous counterparts. Primiparous gray-cheeked mangabey (*Lophocebus albigena*) dams spent more time watching their infants, while their multiparous counterparts spent more time interacting with their infants (Arlet et al., 2019), and Arlet et al. (2021) noted increased

TABLE 7 Results of average models predicting the likelihood of infant survival to (A) 1 month and (B) beyond 1 day for crowned lemurs (*Eulemur coronatus*).

(A)

***E. coronatus*—*N* = 113**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 113**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	−4.877	19.012	(−42.386, 32.632)	.7989
BirthLocCat	Duke	0.17	0			Reference	
	Other			0.068	0.237	(−0.400, 0.536)	.7755
Twin	No	0.41	0			Reference	
	Yes			−0.227	0.387	(−0.990, 0.536)	.5599
DamPar	Mult	1	100			Reference	
	Prim			−2.007	0.825	(−3.642, −0.372)	.0161
SirePar	Mult	1	100			Reference	
	Prim			1.805	0.864	(0.094, 3.517)	.0387
DamCont	No	0.07	0			Reference	
	Yes			0.022	0.168	(−0.311, 0.355)	.8960
BirthYear		0.17	0	0.003	0.010	(−0.016, 0.022)	.7697
Inbreed		0.25	0	0.534	1.249	(−1.926, 2.994)	.6707

(B)

***E. coronatus*—*N* = 113**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 113**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	6.172	19.540	(−32.456, 44.800)	.7542
BirthLocCat	Duke	0.11	0			Reference	
	Other			−0.029	0.192	(−0.408, 0.350)	.8812
Twin	No	0.03	0			Reference	
	Yes			0.009	0.109	(−0.207, 0.225)	.9349
DamPar	Mult	1	100			Reference	
	Prim			−1.841	0.802	(−3.426, −0.256)	.0228
SirePar	Mult	0.44	0			Reference	
	Prim			0.525	0.525	(−1.110, 2.161)	.5292
DamCont	No	0.04	0			Reference	
	Yes			−0.014	0.146	(−0.303, 0.274)	.9232
BirthYear		0.15	0	−0.002	0.010	(−0.021, 0.017)	.8414
DamYear		0.22	0	0.007	0.098	(−0.187, 0.201)	.9408
DamYearSq		0.51	0	−0.003	0.005	(−0.014, 0.008)	.5683
Inbreed		0.09	0	−0.174	0.871	(−1.892, 1.544)	.8424

Note: Only predictors that appeared in the most parsimonious models (ΔAICc < 2) are shown; the predictor was significant for the percent of the most parsimonious models listed (see Supporting Information S1 for further detail). Bolded predictors significantly affected infant survival, based on the *p* value from the averaged model.

Abbreviation: CI, confidence interval.

skill in handling infants with increased experience of female bonnet macaques (*Macaca radiata*), suggesting an improvement in infant care over time that would likely not be evident if the difference were only due to parturition.

Experience with raising offspring, while important in our study in other *Eulemur* species, was not as important in the crowned lemur data set. Crowned lemur infant survival was solely affected by parental experience, but unlike with the collared and

TABLE 8 Results of average models predicting the likelihood of infant survival to (A) 1 month and (B) beyond 1 day for blue-eyed black lemurs (*Eulemur flavifrons*).

(A)							
***E. flavifrons*—*N* = 94**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 59**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	3.761	2.287	(−0.760, 8.281)	.1030
BirthLocCat	Duke	1	100			Reference	
	Other			−2.300	0.743	(−3.787, −0.813)	.0024
DamPar	Mult	0.82	25			Reference	
	Prim			−1.638	1.333	(−4.278, 1.001)	.2237
DamCont	No	0.74	50			Reference	
	Yes			−1.251	1.018	(−3.264, 0.763)	.2234
DamYear		0.26	25	−0.302	0.574	(−1.432, 0.829)	.6009
DamYearSq		0.26	25	−0.014	0.027	(−0.039, 0.067)	.6103
Inbreed		0.17	0	−1.151	4.022	(−9.145, 6.843)	.7778

(B)							
***E. flavifrons*—*N* = 94**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 59**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	2.144	0.766	(0.621, 3.668)	.0058
BirthLocCat	Duke	1	100			Reference	
	Other			−2.045	0.652	(−3.350, −0.740)	.0021
Twin	Yes	0.08	0			Reference	
	No			−0.060	0.328	(−0.713, 0.592)	.8557
DamPar	Mult	0.33	0			Reference	
	Prim			−0.305	0.653	(−1.599, 0.989)	.6441
SirePar	Mult	0.07	0			Reference	
	Prim			0.034	0.281	(−0.527, 0.594)	.9061
DamCont	No	0.18	0			Reference	
	Yes			−0.154	0.443	(−1.030, 0.723)	.7309
DamYear		0.23	0	−0.029	0.068	(−0.164, 0.106)	.6727
DamYearSq		0.19	0	−0.001	0.003	(−0.007, 0.005)	.7168

Note: Only predictors that appeared in the most parsimonious models (ΔAICc < 2) are shown; the predictor was significant for the percent of the most parsimonious models listed (see Supporting Information S1 for further detail). Bolded predictors significantly affected infant survival, based on the *p* value from the averaged model.

Abbreviation: CI, confidence interval.

mongoose lemurs, birthing an offspring had a more significant effect than raising one. Crowned lemur infant survival was significantly improved with increased numbers of births, but not with increased numbers of offspring raised. In contrast, collared and mongoose lemurs did not exhibit improved infant survival with increased births; instead, their infant survival only showed improvement after successfully producing a surviving offspring. This difference aligns with findings in other primate studies. Tardif et al. (1984) found that previous infant-rearing experience improved infant survival rates in common marmosets (*Callitrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*), but while inexperienced marmoset dams showed a 50%–60% infant survival rate, inexperienced tamarin dams showed a 0% infant survival rate; this suggests that experience raising previous offspring is beneficial to both species, but critical to cotton-top tamarins, such that there may be additional factors improving survival for common marmosets. These differences suggest that experience giving birth and experience raising offspring are

TABLE 9 Results of average models predicting the likelihood of infant survival to (A) 1 month and (B) beyond 1 day for mongoose lemurs (*Eulemur mongoz*).

(A)							
***E. mongoz*—*N* = 199**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 156**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	0.369	10.950	(−21.242, 21.980)	.9733
BirthLocCat	Duke	0.28	0			Reference	
	Other			0.151	0.323	(−0.485, 0.786)	.6425
Twin	No	0.35	0			Reference	
	Yes			−0.266	0.510	(−1.269, 0.737)	.6035
DamPar	Mult	1	100			Reference	
	Prim			−1.293	0.423	(−2.128, −0.458)	.0024
BirthYear		0.08	0	0.001	0.005	(−0.010, 0.011)	.9137
DamYearSq		0.08	0	0.000	0.001	(−0.001, 0.001)	.9204
Inbreed		0.79	12.5	−5.012	4.025	(−12.937, 2.912)	.2151

(B)							
***E. mongoz*—*N* = 199**		**Parsimonious models (ΔAICc < 2)**		**Averaged model—*N* = 156**			
Predictors		**Relative importance**	**Percent significant**	**Estimate**	**Standard error**	**95% CI**	***p* Value**
(Intercept)		N/A	N/A	1.761	8.764	(−15.537, 19.059)	.8419
BirthLocCat	Duke	0.36	0			Reference	
	Other			0.250	0.460	(−0.655, 1.155)	.5884
Twin	No	0.04	0			Reference	
	Yes			0.009	0.169	(−0.324, 0.341)	.9595
DamPar	Mult	0.48	0			Reference	
	Prim			−0.415	0.584	(−1.563, 0.732)	.4781
SirePar	Mult	0.04	0			Reference	
	Prim			−0.010	0.117	(−0.240, 0.221)	.9349
DamCont	No	0.22	0			Reference	
	Yes			−0.138	0.366	(−0.859, 0.583)	.7073
BirthYear		0.04	0	0.000	0.004	(−0.008, 0.009)	.9487
DamYear		0.17	0	−0.012	0.036	(−0.083, 0.059)	.7394
DamYearSq		0.14	0	0.000	0.001	(−0.003, 0.002)	.7803
Inbreed		0.95	72.2	−7.186	3.935	(−14.950, 0.577)	.0696

Note: Only predictors that appeared in the most parsimonious models (ΔAICc < 2) are shown; the predictor was significant for the percent of the most parsimonious models listed (see Supporting Information S1 for further detail). Bolded predictors significantly affected infant survival, based on the *p* value from the averaged model.

Abbreviation: CI, confidence interval.

distinct factors that may affect species differently, warranting further study, including in our study species.

Contrary to dam experience, sire experience had a limited impact on infant survival in our study. Crowned lemurs were the only species for which sire experience was significantly associated with infant survival, which is surprising since, of the four species examined, only mongoose lemur sires have been found to actively participate in offspring care in the wild (Tecot et al., 2013). We found that inexperienced sires were associated with increased infant survival. However, only 14 of the 113 crowned lemur infants had parents with differing parity statuses, and all but one of the surviving infants from that group had a multiparous dam and primiparous sire; consequently, sire primiparity is likely confounded with dam multiparity in these situations, leading to the unexpected result.

Unlike dam experience, linear and quadratic dam age did not significantly affect infant survival across species. Collared lemurs tended to be less likely to produce surviving offspring as they aged, which seems counterintuitive to the concept of experienced dams having greater success. Furthermore, multiparous dams tended to be older (7.83 ± 4.47 years) than primiparous dams (5.71 ± 5.26 years). However, the age at first reproduction was higher in primiparous (5.71 ± 5.26 years) than multiparous (3.69 ± 3.79 years) collared lemur dams, indicating that dams without experience also tended to be older dams. Successful crowned lemur dams also first reproduced at a younger age (3.82 ± 2.95 years) than unsuccessful dams (4.68 ± 3.86 years), though not significantly. Since previous experience producing surviving offspring did not significantly affect future success in this species, it appears that there may be some benefit gained by starting reproduction at an earlier age, even if these earlier attempts are less successful. It is possible then that the decreased success in older dams could be an artifact of delayed reproduction, a decision made by zoological managers to limit overpopulation at the facility level, but one that also runs the risk of physiological consequences resulting in decreased reproductive success ("use it or lose it"; Penfold et al., 2014).

The delayed reproductive start in unsuccessful collared lemur dams might suggest a connection to these dams approaching reproductive senescence, as described for ruffed lemurs in Tidière et al. (2018). However, since quadratic age was also not significant, it is possible that another factor, like dam parity, is essentially offsetting the effect of quadratic age. Since older dams are more likely to be multiparous, the lower infant survival rate as the dam approaches reproductive senescence may counterbalance the higher infant survival rate due to having previous experience. Studies of rhesus macaques (*Macaca mulatta*; Gagliardi et al., 2007) and gray-cheeked and black-crested mangabeys (*Lophocebus aterrimus*; de Visser et al., 2022) found decreased infant survival in primiparous or older dams, suggesting a correlation between dam age and parity that was not measurable in our data set. Given the somewhat contradictory findings for collared lemurs that strongly imply a connection between the two, this should be the focus of future studies.

While dam age and previous experience affect infant survival from the physiological and experiential perspective, management-related factors also played a role. Blue-eyed black lemurs were significantly affected by birth location, with the survival rate at Duke Lemur Center more than double that at other facilities. This facility has extensive experience with this species (71 infant births in this study) compared to other facilities (10 infants at the next most experienced facility), potentially leading to their ability to set dams and infants up for success. However, Duke Lemur Center also had noticeably less use of contraception, younger dams, and a greater proportion of dams with previous experience; we initially considered removing birth location from this species' model due to these apparent trends, but retained it due to the lack of statistical correlation between birth location and any of these other variables. The differences between facilities are not particularly surprising; however, as they largely stem from management decisions; blue-eyed black lemur females placed at other facilities tend to be lower on the mean kinship list, are generally older or a lower priority to breed, and are more likely to be previously contracepted.

Collared lemurs did not appear to be affected by birth location but did show a significant improvement in infant survival as birth year increased. We initially predicted that infants with more preceding generations since their most recent wild relative would show lower survival, as seen in some lemur species under human care (Schwitzer & Kaumanns, 2001), and that birth year may indicate changes in management over time, affecting infant survival. The positive impact of birth year suggests that improvements in husbandry and care over time have benefitted this species enough to offset the effect of generations removed from the wild, if one exists for this species. However, though Duke began breeding all species except the mongoose lemur earlier than any other facility (Figure 3), they also showed slightly lower survival rates for those species with a multiyear gap between births (all except blue-eyed black lemurs), so birth location and birth year may be confounded.

Dam contraception was associated with decreased infant survival to 1 month in collared lemurs, though our post hoc analyses could not identify a specific contraception-related factor driving this impact. Average age was higher for previously contracepted collared lemur dams than for noncontracepted dams (9.30 years compared to 6.52 years), as was the age at first reproduction (6.11 years compared to 3.69 years); though dam age and contraception were not correlated, the impact of contraception could simply be an artifact of the higher likelihood of previous contraception in older dams, which were also less likely to produce surviving offspring. Considering the limited impact of contraception on other species, this merits a closer analysis in the future with a more robust data set. Alternatively, since contraceptive use has been suggested to lead to weight gain (Terranova & Coffman, 1997) infant survival could really be negatively associated with increased dam weights. However, since we were unable to incorporate weights into this study, this avenue will need to be explored in the future.

Though some very clear trends were identified in our work, additional factors that we were unable to include in our analysis due to missing data, such as individual dam and sire characteristics and rearing type, might also be important for infant survival. In addition, knowing the infants' cause of death could help identify different predictors of survival for stillborn and other nonsurviving infants and provide actionable suggestions for managers; however, details related to cause of death are rarely documented and thus will be difficult to incorporate into anything but prospective studies. We believe that additional details in this area could help explain why collared lemurs appear to be affected by physiological factors given their early infant mortalities, suggesting a species-specific underlying health issue of the infant or dam (e.g., stillbirths or issues with milk production), but only saw improved infant survival if the dam had previously successfully raised offspring. Future research that focuses on these details would likely require the assistance of, but also be of great benefit to, animal managers and veterinary staff at each facility.

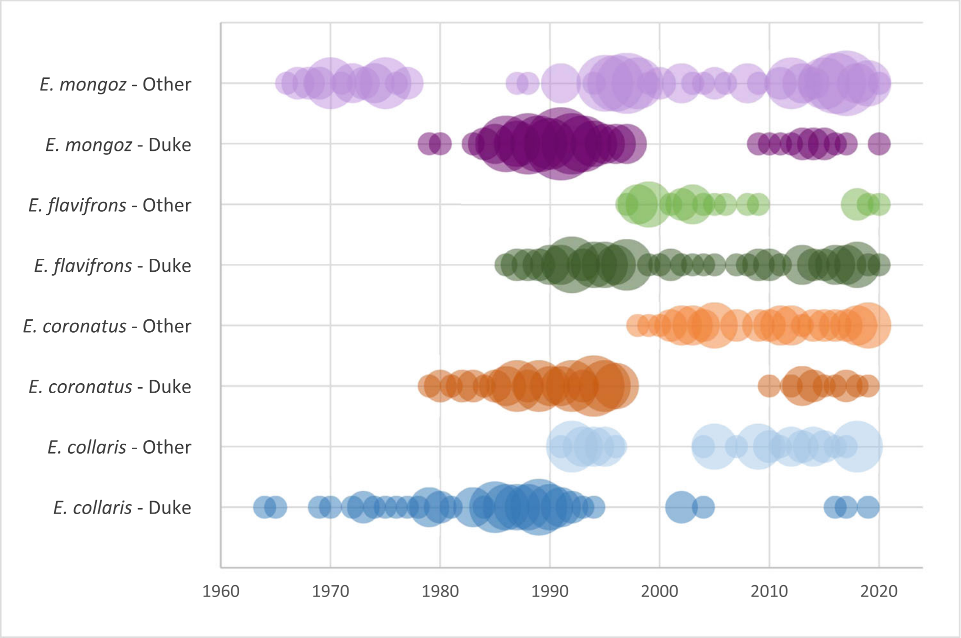

FIGURE 3 Timeline of births for each species at Duke Lemur Center and other facilities. Larger points represent more births, with the largest point representing 10 births for that species/location combination in 1 year.

We focused our post hoc analyses on survival to 1 month, but models for 1-day survival appeared less focused, generally with more factors overall and fewer significant factors (see Supporting Information S1), suggesting higher chance factor in 1-day survival. Regardless of the factors influencing survival, our analyses suggest that opportunities to intervene on behalf of the infant will be limited. When such opportunities arise, preparedness can increase the likelihood of interventions successfully leading to infant survival; helping an infant survive so it may grow to potentially reproduce is generally beneficial, especially for rare species or genetically important individuals (Izard, 2006), despite the decreased reproductive success of hand-reared dams (Niebruegge & Porton, 2006). However, the ability of the individual to positively contribute to the population may be lessened due to lower prioritization for future breeding or decreased maternal care (e.g., Niebruegge & Porton, 2006; Ryan et al., 2002), making hand-rearing a method of last resort. Additionally, since multiparous dams are also more likely to produce surviving infants, and beginning reproduction at an earlier age makes the dam multiparous for more of her lifespan, the likelihood of success can be considered higher for these females when conducting reproductive planning for each population. Identifying females more likely to produce surviving offspring can complement genetic management when determining the recommended number of pairings each year. This creates a need to balance increasing population size with decreasing population genetic diversity, though when the goal is to keep small populations stable or growing, demographic goals may supersede genetic goals.

The results of this study reveal several factors associated with infant survival and offer insights for future research. It is apparent that managers must closely monitor pregnant dams leading up to birth. Although the impact was not significant for all four species, managers should be prepared for potential negative outcomes in dams who have never successfully raised offspring and those whose most recent infant did not survive. This preparedness can be achieved by documenting potential conception dates to predict birthing windows, training reproductive females for ultrasound monitoring during pregnancy, and following the *Eulemur* SSP's birth and rearing guidelines to provide an appropriate environment for the dam and her infant, particularly in the first 30 days of the infant's life, which our data identified as the period in which infants are most vulnerable to mortality.

Future studies that include cause of infant death could inform practical management strategies. Additionally, investigating the relationship between prior contraceptive use and infant survival in collared lemurs, and examining the potential impact of contraception on blue-eyed black lemur infant survival, would be useful to determine if contraception-related management strategies must be altered. Although our use of studbook and contraceptive data provides an initial insight, further research would be benefitted by additional data, more complete records, and most importantly, a larger sample size. Expanding to additional species or incorporating the EAZA populations of these same species could offer more information and avenues of comparison that managers of these additional populations could apply directly to the animals under their care. Similar analyses of additional mammal species could increase our understanding of factors influencing infant survival in other AZA-managed species, which could in turn lead to ex situ population increases for other species of conservation concern and those prioritized for population management by AZA.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available under reasonable request to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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