

The elephant in the family: Costs and benefits of elder siblings on younger offspring life-history trajectory in a matrilineal mammal

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Abstract

1. Many mammals grow up with siblings, and interactions between them can influence offspring phenotype and fitness. Among these interactions, sibling competition between different-age offspring should lead to reproductive and survival costs on the younger sibling, while sibling cooperation should improve younger sibling's reproductive potential and survival. However, little is known about the consequences of sibling effects on younger offspring life-history trajectory, especially in long-lived mammals.
2. We take advantage of a large, multigenerational demographic dataset from semi-captive Asian elephants to investigate how the presence and sex of elder siblings influence the sex, survival until 5 years old, body condition, reproductive success (i.e. age at first reproduction and lifetime reproductive success) and long-term survival of subsequent offspring.
3. We find that elder siblings have heterogeneous effects on subsequent offspring life-history traits depending on their presence, their sex and the sex of the subsequent offspring (named *focal calf*).
4. Overall, the presence of an elder sibling (either sex) strongly increased focal calf long-term survival (either sex) compared to sibling absence. However, elder sisters had higher impact on the focal sibling than elder brothers. Focal females born after a female display higher long-term survival, and decreased age at first reproduction when raised together with an elder sister rather than a brother. Focal males born after a female rather than a male showed lower survival but higher

Vérane Berger and Sophie Reichert shared first authors, equal contributions

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body weight when both were raised together. We did not detect any sibling effects on the sex of the focal calf sex, survival until 5 years old and lifetime reproductive success.

5. Our results highlight the general complexity of sibling effects, but broadly that elder siblings can influence the life-history trajectory of subsequent offspring. We also stress the importance of considering all life stages when evaluating sibling effects on life trajectories.

KEYWORDS

Asian elephant, fitness costs, life-history trade-offs, sex ratio, sibling effects

1 | INTRODUCTION

In all animal societies, the family environment plays a key role in shaping individual phenotype and life-history trajectory (Emlen, 1995; Hudson & Trillmich, 2008). In particular, there may be both costs and benefits associated with having and interacting with siblings. The sibling interactions range from siblicide behaviours (Mock & Parker, 1997) to allomaternal care (Clutton-Brock, 2016) and can induce developmental and survival differences between siblings (Mock & Parker, 1997). These sibling effects can occur within the same litter in polytocous species (Benhaïem et al., 2013; Clark & Galef, 1998; Dupont et al., 2015; Golla et al., 1999; Hudson & Trillmich, 2008; Ryan & Vandenberg, 2002), but also between successive offspring in monotocous species (Clutton-Brock et al., 1983; Leippert et al., 2000; Trillmich, 1986; Trillmich & Wolf, 2008) and are usually sex-specific (Uller, 2006). Nonetheless, despite many vertebrates growing up with siblings, and sibling relationships influencing individual life histories and fitness (Uller, 2006), sibling interactions effects on the life trajectories of subsequent siblings still remains poorly understood. Picking apart the consequences of sibling effects for individual life histories will provide important insights for the evolutionary dynamics within a population.

Competition among siblings sharing early environment is highly common and may entail costs associated with these competitive interactions which will usually depend on the sex of the elder sibling (Mock & Parker, 1997). The negative effects are driven by offspring competing for limited parental resources and care (O'Connor, 1978; Trivers, 1974). In sexually dimorphic mammals where siblings grow up together, the sibling competition can be highly sex-specific (Uller, 2006). The sex-dependent negative effects of siblings stem from the fact that female and male offspring differ behaviourally, morphologically, physiologically and genetically, implying higher energetic needs in growth and survival in one sex over another (Clutton-Brock, 2016). In monotocous species in particular, because of size and behavioural dominance, a competitive advantage of the elder sibling for the parental resources is expected over the younger one (Trillmich & Wolf, 2008). Still, in such monotocous and social species with overlapping reproductive events, long offspring dependency, slow maturation and late dispersal (e.g. humans; Nitsch

et al., 2013), such sex-specific sibling effects can affect future offspring condition and fitness (Clutton-Brock & Sheldon, 2010) through two phenomena. First, younger siblings may be affected by the depletion of maternal condition, where the higher energetic costs of producing one sex over the other may imply a reduced ability of mothers to allocate resources to subsequent offspring (Koivula et al., 2003; Martin & Festa-Bianchet, 2010). For example, offspring of mothers who had produced a son in the previous reproductive event displayed lighter early-life body mass (in bighorn sheep *Ovis Canadensis*; Bérubé et al., 1996); humans (Rickard, 2008); Galapagos fur seals *Arctocephalus galapagoensis*, sea lions *Zalophus wollebaeki* (Trillmich & Wolf, 2008), lower reproductive success (humans, Rickard et al., 2007) and reduced survival (in Galapagos fur seals, Nager et al., 2000). Furthermore, mothers can have longer birth intervals after producing a son (Lee & Moss, 1986). In bighorn sheep *O. canadensis*, the year after weaning (the more costly) sons, ewes were more likely to have a daughter than a son if in poor condition (Douhard et al., 2016). Second, in species with overlapping reproductive events, direct sex-specific sibling interactions have important developmental, morphological or behavioural consequences affecting survival and reproductive success of other offspring (Hudson & Trillmich, 2008; Uller, 2006). For example, in wolves, the presence of previously weaned offspring diminished lifetime reproductive success in focal males compared to their absence (Sparkman et al., 2011). In humans, reproductive success in both sexes was reduced by same-sex elder siblings (Borgerhoff-Mulder, 1998), especially if they were present still after sexual maturity (Nitsch et al., 2013), although these trends are not always observed in contemporary societies (Lawson & Mace, 2009).

Although sibling relationships have traditionally been investigated in the context of negative effects (Hudson & Trillmich, 2008; Mock & Parker, 1997), sibling interactions can also result in beneficial effects (Arnold & Owens, 1998; Jennions & Macdonald, 1994; Sparkman et al., 2010). Indeed, while competing with a sibling can bring direct fitness benefits via increased own size, survival or reproductive opportunities, it also increases drastically the indirect fitness costs via decreased kin survival and reproduction (Parker et al., 1989). In such a context, kin selection should moderate sibling competition and favour cooperative behaviours when the

benefits of helping a sibling exceed its costs (Hamilton, 1964; Parker et al., 1989). Cooperation to share food or provide protection has beneficial consequences on the subsequent offspring. For instance, in highly social and cooperative breeders, such cooperative behaviours from helpers—which are often offspring born in previous years—have positive effects on juveniles' growth, reproduction and survival (Jennions & Macdonald, 1994; Koenig & Dickinson, 2016; Salomon & Lubin, 2007). However, associations between siblings may be particularly complex in social species with high cognitive capabilities but have been little-studied to-date (Uller, 2006). Overall, we currently have a poor understanding of sex-specific sibling costs and benefits on the life trajectories of subsequent siblings despite the role of sibling relationships in shaping individual life histories and fitness in many vertebrates (Uller, 2006).

Particularly, the long-term consequences resulting from the sibling effects remain understudied (Roulin & Dreiss, 2012). One issue is that so far empirical studies have concentrated on short-term observations and not explored beyond independence, which may limit our understanding of the intragenerational costs of sibling effects, especially if such costs are not apparent until offspring are reproductively mature (Nitsch et al., 2013; Sparkman et al., 2010). Logistic of field studies can constrain investigations of these costs over the entire lifetime of offspring. However, sibling effects could also vary depending on the trait considered and on the life stage of the individual (Bebbington et al., 2017; Clutton-Brock & Sheldon, 2010; Nitsch et al., 2013; Sparkman et al., 2010). For instance, elder siblings may improve the survival of younger offspring through alloparental care, but then reduce reproductive success after sexual maturity through competition (Nitsch et al., 2013). Longitudinal data that include several fitness-related traits spanning over the lifetime of offspring is therefore key if we are to understand the fitness consequences of sibling effects, and thus the evolution of this process. In addition, given that life-history theory predicts that maternal reproductive effort should increase with age as reproductive value decreases (Stearns, 1992), and that selection may favour adjustment of offspring sex ratio according to the age of parents (Trivers & Willard, 1973), offspring life-history traits might also vary with the age of the parents. Because of such variation, it is crucial to account for parental age and quality when investigating subsequent offspring life trajectories.

Here, we assess the effect of the elder sibling on offspring life-history trajectories in Asian elephants *Elephas maximus*. Elephants provide a promising opportunity to test several key predictions of sibling interactions on offspring fitness for a long-lived species. Well known for their marked sexual dimorphism in weight and height, males are bigger and heavier (Chapman et al., 2016), grow faster, have higher juvenile mortality and need more care from their mothers (Lahdenperä et al., 2015). In wild African elephants *Loxodonta africana*, birth intervals are also longer after a male birth than a female birth (Lee & Moss, 1986). In Asian elephants, after a pregnancy of nearly 2 years, mothers allocate energy in lactation for several years, and average birth intervals are around 5 years in

natural living environments (Lahdenperä et al., 2014). Furthermore, because females stay in their family groups and males only disperse in adolescence around age 10, mothers can simultaneously care for several calves, which may display both competitive and cooperative interactions (Sukumar, 2003). Indeed, there is compelling evidence for cooperative behaviours between females leading to increased fecundity and survival (Lynch et al., 2019; Sukumar, 2003). Moreover, males have been found to be more aggressive and competitive than females (Seltmann et al., 2019). Such observations reinforce the idea that elder sisters should have positive effects on the subsequent calf life-history traits and elder brothers should have negative effects.

The present study aims to investigate sex-specific sibling effects on a suite of different life-history traits linked to fitness (body mass, reproduction traits and survival rates) in the matrilineal system of Asian elephants, to determine the fitness consequences for subsequent siblings. We take advantage of a large, unique multigenerational demographic dataset of a semi-captive population of Asian elephants from timber camps in Myanmar, for which maternal and offspring life trajectories are known accurately. We tested sibling effects on the sex, body mass and reproductive traits (i.e. age at first reproduction and lifetime reproductive success) of subsequent siblings. To do so, we tested the effect of the interaction between the sex of the elder sibling, the sex of the focal sibling and their concurrent presence on focal calf life-history traits. We explored the effect of the previous offspring presence and sex on survival of focal calves (a) up to weaning age (until 5 years) and (b) from 6 years. In the study population, calves are separated from their mothers and tamed between the ages of 4 and 5. Calves from two breeding attempts may therefore simultaneously be under maternal care, and able to compete. To account for potential maternal effects, for all calf traits, we accounted for the effects of maternal age as a determinant of maternal condition (Festa-Bianchet et al., 1998; Nussey et al., 2008; Reichert et al., 2020). However, because of the strong correlation between the concurrent presence of both siblings and birth interval, and because of the lack of data on maternal body condition, our study cannot fully disentangle maternal allocation from sibling competition (see Section 2).

We predict that (a) given the apparent cost of producing males in dimorphic mammals (Douhard et al., 2016; Rickard et al., 2007; Trivers & Willard, 1973), more females than males will be produced after elder brothers. (b) Early-life traits such as calf survival to the age of 6 and body mass should be increased in the presence of elder sisters and decreased in the presence of elder brothers. As found in other highly social species, competitive behaviours between siblings lead to reduced reproductive potential and life span while cooperative behaviours lead to improved reproduction and life span. Therefore, (c) female age at first reproduction should be delayed and female lifetime reproductive success should be decreased in the presence of elder brothers. Moreover, (d) calf survival from 6 years old should be increased in the presence of elder sisters and decreased in the presence of elder brothers during early life.

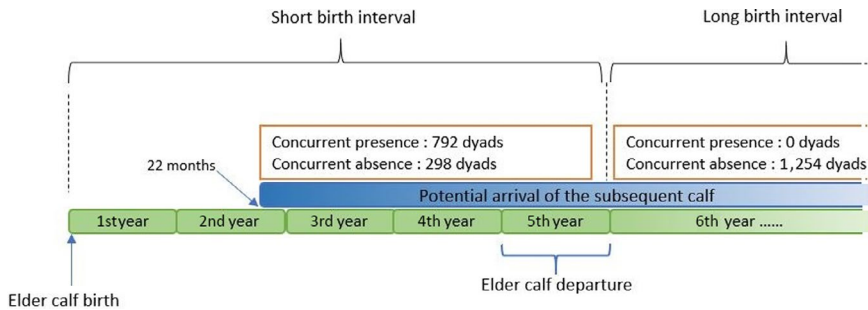


FIGURE 1 Illustrative schema of the relationship between the concurrent presence of the dyad of the elder and focal siblings. As the gestation time is 22 months, this duration is the shortest birth interval

2 | MATERIALS AND METHODS

2.1 | Study population

This study was conducted on government-owned Myanmar timber elephants that inhabit forest camps, distributed across Myanmar and considered 'semi-captive'. The elephants are used during the day as riding, transport and draft animals. The Myanmar Timber Enterprise (MTE) imposes regulations on the daily and annual workload of elephants, which are consistent for all individuals in the study population (Zaw, 1997).

During the night, the elephants forage in the forest, unsupervised, and may interact and mate with both wild and tame conspecifics. There are no husbandry procedures. Timber elephants are never culled. Calves born in captivity are cared for and nursed by the biological mother and allomothers (Lahdenperä et al., 2018; Lynch et al., 2019). Therefore, breeding rates are natural with no reproductive management. Moreover, there is minimal food provisioning. Although elephants benefit from veterinary care, only traditional medicines were available during most of the study period. The workload is adjusted for pregnant females and new mothers. Reproductive females are rested from mid-pregnancy (11 months into gestation) until the calves reach their first birthday. Mothers are then used for lighter work duties until the calf reaches age 4. Calves are separated from their mother and tamed at around the age of 4 or 5 (Oo, 2010), at which point they are assigned a rider, name, logbook and registration number. After the training period, elephants are used for light work duties until the age of 17, when they enter the full workforce until retirement at 55. The MTE maintains their logbooks until death.

The dataset, collated from logbooks and annual extraction reports of MTE, includes the identification number and name of each animal, birth origin (captive-born or wild-caught), date of birth, latest location, mother's identification number and name, year and place of capture (if wild-captured), date of death or last known date alive. For wild-caught mothers, the capture age (and thus approximate birth year) is estimated by comparing their height and body size with captive-born elephants of known age and through morphological assessment (Lahdenperä et al., 2018).

2.2 | Data selection

Our dataset included captive-born calves with a known mother, an elder sibling of known sex and known survival status, and

which had complete records for birth date, birth origin, sex and last seen date leading to a sample size of 2,623 focal calves. The exact age of death was not known for all calves in the dataset because calves were still alive at the end of the study or were not followed until the end of the study (censored life spans). For 276 of the 2,623 focal calves, the censored longevity of the elder calf was lower than the following birth interval preventing us from assessing the concurrent presence/absence of both successive siblings with certainty, and these cases were therefore excluded from our analyses. We removed also all focal calves that were stillborn (i.e. gestation complication not likely to be caused by the elder sibling, $N = 44$). This demographic sample included 2,344 calves ($F = 1,158$, $M = 1,186$) born between 1945 and 2018 (1,057 mothers). In all, 1,159 calves were still alive at the end of the study and 460 were not followed until the end of the study. In addition to demographic data, the weight (kg) of elephants monthly measured between December 2011 and June 2017, and all elephants were measured in mornings on non-working days. Weight was measured using EziWeigh 3000 scales, and was recorded to the nearest 1 kg (Mumby et al., 2015).

2.3 | Concurrent presence/absence of siblings during rearing

We considered all calves for which we had at least the identity and the sex of their elder sibling. We determined whether calves were reared in the presence of their older sibling as a binary variable. In this context of a semi-captive population where calves are separated from their mothers around 4 or 5 years old (Crawley et al., 2020), we have only dyads of siblings growing up together. The focal individual is always the youngest in a dyad. We assessed the time in years that the elder and focal calf spent together before taming (the average time siblings raised together was 1.85 ± 0.96 years). Both siblings were raised together when the birth interval was shorter than 6 years and when the elder sibling was alive at the time the next sibling was born and raised. Both siblings were not raised together when (a) the birth interval was shorter than 6 years but the elder sibling died before the birth of the next sibling and (b) when the birth interval was over 5 years (Figure 1, Supporting Information A and B for details). In the subset of calves with birth intervals <5 years, we tested the effect of the number of years raised together (see Supporting Information E).

TABLE 1 Sex-specific models of elder calf using Generalized Mixed Models. *Base* corresponds to the model including confounding variables (see Table B2 in Supporting Information B). *Concurrent* corresponds to the presence/absence of both the elder and focal calf during weaning. The number of parameters is indicated by *k*. The competitive models are in bold. The model with highest predictive performance is highlighted in grey

Trait	Model	<i>k</i>	AIC	ΔAIC	AICw
Focal calf sex	Base	6	3,252.43	0.00	0.43
2,344 focal calves	Base+Elder sex	7	3,253.73	1.30	0.22
1,057 mothers	Base+Concurrent	7	3,254.05	1.62	0.19
	Base+Elder sex+concurrent	8	3,255.33	2.90	0.10
	Base+Elder sex*concurrent	9	3,256.26	3.82	0.06
Focal calf body mass	Base+Focal sex*Elder sex*Concurrent	21	12,053.57	0.00	1.00
144 focal calves	Base+Focal sex*Concurrent+Elder sex	18	12,083.31	29.74	<0.01
2,734 measurements	Base+Focal sex*Elder sex+Concurrent	18	12,084.00	30.42	<0.01
87 mothers	Base+Focal sex*Elder sex	17	12,092.47	38.90	<0.01
	Base+Focal sex+Elder sex+Concurrent	17	12,093.05	39.48	<0.01
	Base+Focal sex+Elder sex	16	12,101.57	48.00	<0.01
	Base+Concurrent	15	12,107.96	54.39	<0.01
	Base+Elder sex	15	12,108.81	55.23	<0.01
	Base+Focal sex	15	12,109.25	55.68	<0.01
	Base	14	12,116.48	62.91	<0.01
Focal female AFR	Base+Elder sex*Concurrent	11	1,626.91	0.00	0.62
258 focal females	Base+Elder sex+Concurrent	10	1,630.59	3.68	0.10
213 mothers	Base+Elder sex	9	1,630.66	3.75	0.10
	Base+Concurrent	9	1,630.68	3.77	0.09
	Base	8	1,630.75	3.84	0.09
Focal female LRS corrected for AFR	Base	10	837.30	0.00	0.48
	Base+Elder sex	11	838.91	1.61	0.21
258 focal females	Base+Concurrent	11	839.12	1.82	0.19
213 mothers	Base+Elder sex+Concurrent	12	840.74	3.44	0.08
	Base+Elder sex*Concurrent	13	842.61	5.31	0.03
Focal female LRS not corrected for AFR	Base	9	859.54	0.00	0.50
	Base+Concurrent	10	861.35	1.81	0.20
258 focal females	Base+Elder sex	10	861.49	1.95	0.19
213 mothers	Base+Elder sex+Concurrent	11	863.30	3.76	0.07
	Base+Elder sex*Concurrent	12	864.62	5.08	0.04
Focal calf survival to 5 years of age	Base	9	2,116.66	0.00	0.32
	Base+Focal sex	10	2,118.39	1.73	0.13
2,344 focal calves	Base+Focal sex*Elder sex	12	2,118.41	1.75	0.13
1,057 mothers	Base+Elder sex	10	2,118.66	2.00	0.12
	Base+Concurrent+Focal sex*Elder sex	13	2,119.07	2.41	0.10
	Base+Concurrent	10	2,119.39	2.73	0.08
	Base+Focal sex+Elder sex	11	2,120.41	3.75	0.05
	Base+Concurrent+Focal sex+Elder sex	12	2,121.16	4.50	0.03

(Continues)

TABLE 1 (Continued)

Trait	Model	<i>k</i>	AIC	ΔAIC	AICw
	Base+Concurrent*Elder sex+Focal sex	12	2,122.87	6.21	0.01
	Base+Concurrent*Focal sex+Elder sex	12	2,123.00	6.34	0.01
	Base+Concurrent*Focal sex*Elder sex	15	2,123.10	6.44	0.01
Focal calf longevity	Base+Concurrent+Focal sex*Elder sex	29	2,363.01	0.00	0.49
1,251 focal calves	Base+Concurrent+Focal sex+Elder sex	28	2,365.46	2.44	0.15
704 mothers	Base+Concurrent*Elder sex+Focal sex	29	2,365.86	2.85	0.12
	Base+Concurrent*Focal sex+Elder sex	29	2,366.55	3.53	0.08
	Base+Concurrent*Focal sex*Elder sex	32	2,366.74	3.73	0.07
	Base+Focal sex*Elder sex	28	2,368.33	5.32	0.03
	Base+Focal sex	25	2,368.94	5.92	0.02
	Base+Focal sex+Elder sex	27	2,370.92	7.91	<0.01
	Base+Concurrent	26	2,374.26	11.25	<0.01
	Base	25	2,379.49	16.48	<0.01
	Base+Elder sex	26	2,381.39	18.37	<0.01

2.4 | Statistical analysis

We performed our analyses using the R software package, version 3.5.2 (R CoreTeam, 2018).

2.4.1 | Dependent variables

First, to investigate the effect of the elder sibling sex and presence on focal calf sex ($N = 2,344$ focal calves including 792 calves raised together from 1,057 mothers), we included focal calf sex as a dependent variable with a binomial error distribution (female = 0, male = 1). Second, to investigate the effect of elder sibling sex and presence on focal calf survival to 5 years old (2,344 focal calves, exact life span = 725, censored life span = 1,619, 1,057 mothers), we included the focal calf survival to 5 years as a dependent variable with a binomial error distribution (death = 0, alive = 1). Third, to investigate the effect of elder sibling sex on focal calf body mass during the growth period, we analysed 2,734 measures of weight for 144 calves of both sexes (87 mothers) aged from 0 to 20 years old (end of growth; Mumby et al., 2015). Because calf age is closely linked to mass and we had longitudinal observations from calves of different ages, we used standardized weights as the dependent variable. Using a standardized weight enabled us to compare each observation to the expected population-level weight at a given age, and thus to compare observations from calves of different ages. The standardized weights were the residuals from monomolecular

growth curves fit between age and body weight using the *nls* function with the self-starting function *SSasymp* in R. We selected a monomolecular growth function to reflect the precocial life history of elephants, with an immediate exponential increase in body mass early in life before reaching an asymptote (Gaillard et al., 1997). Separate curves were used for males and females, which display differences in morphology; males are typically larger with a mean final shoulder height of 242 cm and a mean adult body mass of 3,273 kg compared to 220 cm and 2,548 kg for females, respectively (Mumby et al., 2015).

Fourth, we assessed the effect of elder sibling sex and presence in early life on female subsequent reproductive output, namely, age at first reproduction (AFR) and lifetime reproductive success (LRS) measured as the number of live-born calves produced by a female throughout her lifetime. We did not assess male reproduction because father identity is currently unknown. We investigated AFR (258 calves from 213 mothers) as a dependent variable with a Gaussian distribution. We investigated focal female offspring LRS (258 calves, 213 mothers) using a Poisson error distribution (see Supporting Information B for the fit of the distributions of AFR and LRS). Fifth, to investigate the effect of elder sibling sex and its presence on focal calf survival after the age of 5 (range: 6–55 years old, $N = 1,251$, observed longevity: 203 focal calves, censored longevity: 1,048 focal calves, 704 mothers), we modelled focal calf survival as a function of time to death using accelerated failure time (AFT) with a lognormal distribution (see Supporting Information B for details). We separated the analyses of the effect of the elder

TABLE 2 Output of the retained models of focal calf sex and standardized body mass by the model selection (see Table 1). We provide the estimates, SE, Z-value, p-value and T-value

Dependent variable	Estimate	SE	Z	P	T
Focal calf sex					
Intercept	-0.27	0.19	-1.43	0.15	—
Mother origin	0.06	0.10	0.66	0.51	—
Birth order	0.07	0.04	1.80	0.07	—
Maternal age	-0.002	0.006	-0.23	0.81	—
Birth interval: Long	0.02	0.01	1.38	0.17	—
Birth interval : Short	0.001	0.03	0.04	0.97	—
Focal calf standardized body mass					
Intercept	-277.25	311.63	—	—	-0.89
Focal sex	-94.86	70.51	—	—	-1.35
Elder sex	-4.65	76.24	—	—	-0.06
Concurrent	-17.27	97.68	—	—	-0.18
Focal sex: Elder sex	122.33	105.30	—	—	1.16
Focal sex: Concurrent	177.79	119.47	—	—	1.49
Elder sex: Concurrent	22.78	126.41	—	—	0.18
Focal sex: elder sex: Concurrent	-178.31	166.08	—	—	-1.07
Measure season_hot	-4.70	8.61	—	—	-0.55
Measure season_monsoon	21.45	9.07	—	—	2.36
Birth order	1.96	15.42	—	—	0.13
Maternal age	11.80	17.38	—	—	0.68
Maternal age ²	-0.11	0.23	—	—	-0.48
Mother origin	-19.85	47.40	—	—	-0.42
Birth interval : Long	-1.65	6.74	—	—	-0.25
Birth interval : Short	1.58	18.68	—	—	0.08

sibling on focal calf survival between 0 and 5 and from 6 years old because of the high calf mortality in this population (Lahdenperä et al., 2014).

2.4.2 | Base models

In the *base model*, we included mother age (14–78 years) at the birth of the focal calf in a dyad following (Reichert et al., 2020; see Supporting Information B for the details of the inclusion of maternal age in models for each focal calf traits), mother origin (wild-caught or captive-born; Lahdenperä et al., 2014) and birth order of the focal calf (Mar et al., 2012) which corresponds to maternal parity (varying between 2 and 11). Although the birth interval (varying between 2 and 41 years) between the elder and focal calf is likely to influence the focal calf trajectories (Mar et al., 2012), a strong correlation occurred between the birth interval and the presence of the elder calf (Figure 1, see Supporting Information A). Indeed, siblings had no chance to be raised together when the birth interval was longer than 5 years. We thus distinguished short and long birth intervals (see Supporting Information B for details). In all models, we included the identity of the mother as a random intercept to account

for non-independence of different calves from the same mother. In addition, because there were repeated measures for each focal individual in the standardized body mass models, we also included focal calf ID as a random intercept. The region and the birth cohort of 5 years (a categorical factor corresponding to the birth lustrum of each calf from 1945 to 2018 created to avoid levels [years] with too few observations) were also included as random factors to account for geographical and temporal variation in vital rates (Jackson et al., 2019). For details in the models, see Supporting Information B.

2.4.3 | AIC-based model selection

We compared the predictive performance of the *base model* to models including the effects of one-way, two-way and three-way interactions of the elder sibling sex, the focal calf sex and the concurrent presence of the siblings during rearing using the Akaike information criterion (AIC), considering each random effect as one parameter (Pinheiro & Bates, 2000). When investigating the effect of the elder sibling's sex on the focal calf's sex, we tested only the interaction between elder sibling sex and the concurrent presence of both siblings. For LRS, we also assessed the predictive performance by including

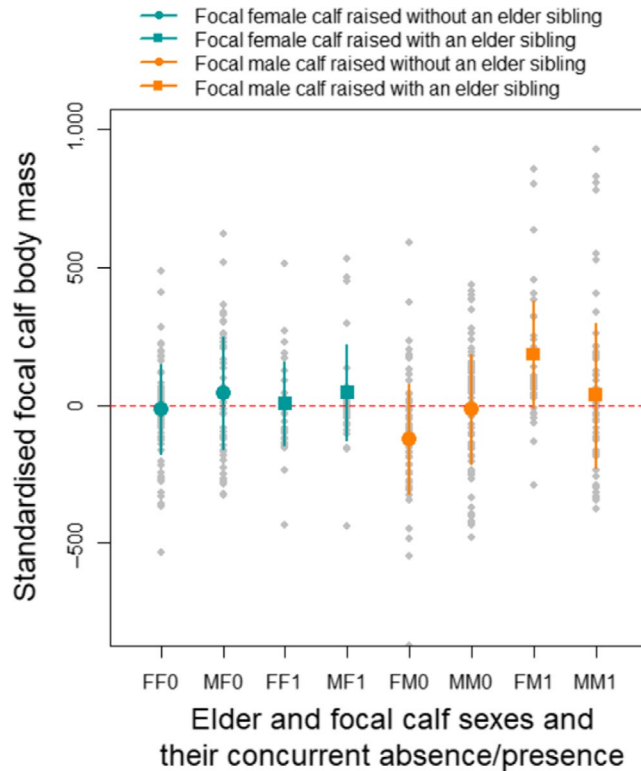


FIGURE 2 Focal calf standardized body mass as a function of both the elder (first letter) and focal calf (second letter) sex (F: female, M: male), and their concurrent presence (0: absence, 1: presence). Grey points indicate the observed standardized body masses. Green points are the mean predicted standardized body masses of focal female calves raised without an elder sibling. Green squares are the mean predicted standardized body masses of focal female calves raised concurrently with an elder sibling. Orange points are the mean predicted standardized body masses of focal male calves raised without an elder sibling. Orange squares are the mean predicted standardized body masses of focal male calves raised concurrently with an elder sibling. Error bars are the associated standard deviations for each group. Predictions were obtained from the model fitting an interaction between the elder calf sex, the focal calf sex and their concurrent presence during rearing (Table C1)

or excluding AFR to test whether any LRS differences were mediated by differences in AFR, or in fertility rate throughout reproductive life. We retained the model with the lowest AIC as the best model. Where the difference in AIC between competing models was less than two, we retained the most parsimonious model with fewest parameters (Burnham & Anderson, 2002). We calculated the Akaike weight (AICw) for each model to provide the relative likelihood that the model was the best among the candidate models.

We fitted models of focal calf survival from 6 years old using Accelerated Failure Time (AFT) models (package: `SURVIVAL` function: `'survreg'`, Therneau & Lumley, 2014). AFT models offer an alternative to proportional hazard (PH) approaches when modelling survival data. The AFT approach models survival times and provides a

summary measure that is interpreted in terms of longer or shorter lives (Swindell, 2009). Indeed, AFT models assume a multiplicative effect of the covariate on survival time where $\gamma = \exp(\beta)$ is the acceleration factor and represents a ratio of time-quantile (Kleinbaum & Klein, 2010). Therefore, γ describes how a covariate stretches out or contracts survival time (see Supporting Information B). We fitted body mass and AFR models using linear mixed models and focal calf sex, survival to 5 years and focal sister's LRS using generalized mixed models (package: `LME4` function: `'lmer'` and `'glmer'`, Bates et al., 2015).

3 | RESULTS

3.1 | Focal calf sex

The overall birth sex ratio in the study sample was even, with 49.40% of the focal calves being females. The elder calf sex did not have a detectable effect on the sex of the focal calf ($\beta_{\text{elder sex} \times \text{presence}} = -0.18 \pm 0.17$, Tables 1 and 2). If the mother had previously produced a son, 49% (± 0.02) of the following calves were females, and if the mother had previously produced a daughter, 50% (± 0.02) of the calves produced next time were females. Although birth interval differences could occur between and within mothers (average birth intervals: 6.77 ± 4.14 years), our result was unlikely influenced by these differences that were tested and controlled for in the models (Table 2 and Table C1).

3.2 | Focal calf body mass during growth period

We found that the standardized body mass of focal calves varied in response to their own sex, the sex of their elder sibling and elder sibling presence or absence during rearing. This variation in standardized body mass was supported by a three-way interaction between elder calf sex, focal calf sex and the concurrent presence of both siblings (Figure 2; Tables 1 and 2). When the focal calf was a female, we did not find differences in standardized body mass depending on the sex and the presence of an elder sibling (green points on Figure 2; $\beta_{\text{elder male}} = -4.65 \pm 76.24$; $\beta_{\text{presence}} = -17.27 \pm 97.68$). In contrast, focal male body mass was strongly affected by the sex and the presence of elder siblings (orange points on Figure 2). On average, males raised with their elder sister displayed the highest average value of standardized body mass (77.26 ± 105.0 ; $\beta_{\text{elder female:focal male:present}} = 178.49 \pm 166.11$), and the lowest values were displayed by males not raised with their elder sister (-83.25 ± 102.0). For males that were not raised with an elder sibling, those with an elder sister were lighter than those with an elder brother ($\beta_{\text{elder male:focal male:absent}} = 128.01 \pm 109.41$). Contrary to expectations from other studies on ungulates, males raised with their elder brother did not show any standardized body mass differences compared to those without (Table 2).

TABLE 3 Output of the retained models of focal female age at first reproduction (AFR) and lifetime reproductive success (LRS) by the model selection (see Table 1). We provide the estimates, SE, Z-value, p-value and T-value

Dependent variable	Estimate	SE	Z	p	T
Focal female AFR					
Intercept	23.29	1.87	—	—	12.49
Elder sex	-0.24	0.86	—	—	-0.28
Concurrent	-1.34	1.32	—	—	-1.01
Elder sex: Concurrent	2.48	1.39	—	—	1.79
Birth order	-0.12	0.28	—	—	-0.42
Mother origin	-0.13	0.74	—	—	-0.17
Birth interval: Long	-0.14	0.13	—	—	-1.02
Birth interval: Short	-0.45	0.34	—	—	-1.35
Focal female LRS not corrected for AFR					
Intercept	1.01	0.21	4.84	<0.01	—
Censor	-0.08	0.15	-0.52	0.60	—
Birth order	-0.05	0.04	-1.27	0.20	—
Mother origin	0.08	0.11	0.70	0.49	—
Mother age class (22–28)	-0.19	0.16	-1.17	0.24	—
Mother age class (29–37)	-0.29	0.17	-1.67	0.09	—
Mother age class (38+)	-0.20	0.20	-0.99	0.32	—
Birth interval: Long	0.007	0.02	0.45	0.65	—
Birth interval: Short	0.03	0.03	0.73	0.46	—
Focal female LRS not corrected for AFR					
Intercept	1.91	0.28	6.90	<0.01	—
AFR	-0.04	0.01	-4.77	<0.01	—
Censor	-0.25	0.15	-1.65	0.10	—
Birth order	-0.07	0.04	-1.62	0.10	—
Mother origin	0.08	0.11	0.71	0.48	—
Mother age class (22–28)	-0.18	0.16	-1.12	0.26	—
Mother age class (29–37)	-0.26	0.17	-1.50	0.13	—
Mother age class (38+)	-0.17	0.20	-0.86	0.39	—
Birth interval: Long	0.003	0.02	0.16	0.87	—
Birth interval: Short	0.01	0.04	0.41	0.68	—

3.3 | Focal female reproduction

Focal female AFR varied from 8 to 40 years with a mean of 21.22 ± 5.78 years (258 focal females). Focal female AFR was influenced by the concurrent presence of the elder sibling (Tables 1 and 3; Figure 3). Females raised with an elder sister reproduced for the first time on average 2 years earlier when compared to females with an elder brother ($\beta_{F1-M1} = 2.24 \pm 1.11$). While not a significant effect, females raised with an elder sister also had slightly earlier AFRs compared to females with an elder sister but not raised together ($\beta_{F1-F0} = 1.34 \pm 1.30$). However, females raised in the presence/absence of elder brothers did not differ in their AFR ($\beta_{M1-M0} = 1.14 \pm 1.31$). Focal female LRS varied from 1 to 8 calves with a mean of 2.12 ± 1.38 calves. Neither the sex of the elder sibling ($\beta_{elder\ sex} = 0.02 \pm 0.09$) nor concurrent presence ($\beta_{presence} = -0.06 \pm 0.14$) affected focal female LRS. This result remained unchanged when including AFR as a covariate (Table 1).

3.4 | Focal calf survival

(a) We did not find any effects of the elder sibling sex or the concurrent presence of both siblings on the focal calf survival to 5 years ($\beta_{elder\ sex} = -0.003 \pm 0.12$; $\beta_{focal\ sex} = -0.06 \pm 0.12$; $\beta_{presence} = -0.21 \pm 0.18$, Tables 1 and 4). (b) Overall focal calf longevity showed a mean of 23.77 ± 12.70 years old. We found an interaction between elder sibling sex and focal calf sex on focal calf survival after age 5 ($\Delta AIC = 2.44$ compared to the following model, Tables 1 and 4; Figure 4). We also detect a strong positive effect of the presence of the elder sibling (female or male) as an additive term ($\gamma_{absence-presence} = 1.63[1.36; 1.95]$, here $\gamma = \exp(\beta)[\exp(\beta - sd); \exp(\beta + sd)]$) on focal calf survival (both sexes) after age 5. Focal female calves with an elder sister had longer lives than focal male calves with an elder sister ($\gamma_{FF-FM} = 0.51[0.43; 0.61]$; red/green lines in Figure 4). Focal females with an elder brother showed longer lives than focal males with an elder sister ($\gamma_{FM-MF} = 1.51[1.28; 1.78]$;

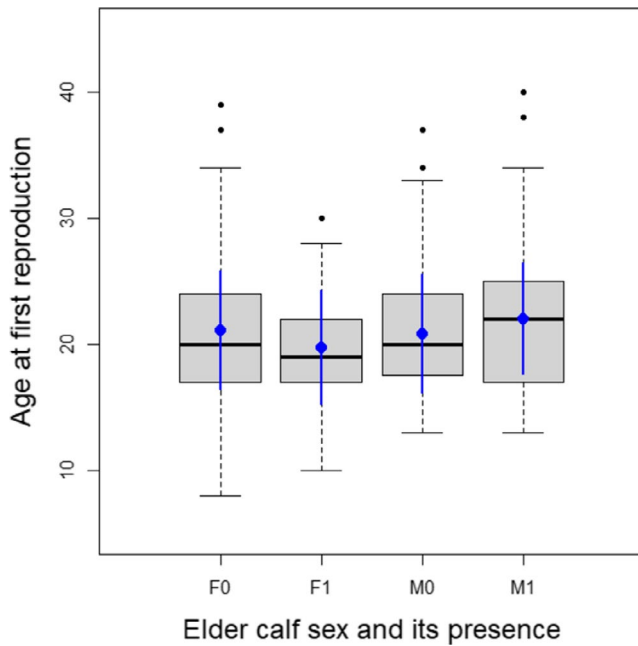


FIGURE 3 Variation of focal sister's age at first reproduction with the elder sibling sex (F: female, M: male) and its concurrent presence (0: absence, 1: presence). Boxplots represent the distributions of observed ages at first reproduction for each sibling sex/concurrent presence group. Blue points and the associated error bars represent the predicted age at first reproduction and the associated standard deviations

blue/green lines in Figure 4). For focal females, having an elder sister slightly increased longevity compared to having an elder brother ($\gamma_{FF-MF} = 0.77[0.65; 0.92]$; red/blue lines in Figure 4). In contrast, for focal males, having an elder brother slightly increased longevity compared to having an elder sister ($\gamma_{FM-MM} = 1.28[1.09; 1.51]$; green/purple lines in Figure 4).

4 | DISCUSSION

Our study provides a comprehensive assessment of the impact of sibling effects on a suite of offspring life-history traits linked to fitness in a long-lived mammal. We highlight the general complexity of sibling effects on subsequent offspring life-history trajectories. As expected, sibling effects on focal calf life-history traits depended on the sex of the focal offspring, on the sex of the elder sibling, and whether they were raised together. We observed sibling effects on focal calf body mass, focal female age at first reproduction and focal calf survival from 6 years old. Interestingly, elder sisters had a stronger impact than elder brothers on subsequent calf life-history traits. Indeed, following our (prediction 2), we showed that elder sisters increased their younger brother's body mass when they were raised together. Elder sisters also had a positive impact on the age at first reproduction of younger sisters when raised together, moderately advancing it (prediction 3). Overall, elder sibling presence (regardless of their sex) strongly increased calf survival from 6 years old

(both sexes). In accordance with the (prediction 4), elder sisters had a strong positive effect on focal female survival. However, contrary to our expectation, elder sisters had a negative effect on focal male survival. Further analyses testing the effect of the number of years raised together ran on a smaller subset of individuals displaying birth interval <5 years confirmed our results (see Supporting Information E). Surprisingly, we did not detect any sibling effects on the focal calf sex (prediction 1), survival to 6 years old (prediction 2) and female lifetime reproductive success (prediction 3). Overall, our study suggests both costs and benefits from elder siblings, with beneficial effects being greater than costs, might indicate that cooperation effects prevail over competition effects in shaping calf life-history trajectory in Asian elephants.

The presence of an elder sister was associated with benefits to longevity (increased) and age at first reproduction (decreased) for females, suggesting that elder sisters improved the reproductive potential of subsequent female siblings. However, this beneficial effect was not found for lifetime reproductive success. This surprising result could be due to the low sample size of females for which we had the full reproductive history (25 focal sisters) which likely prevented us from detecting the effect of elder siblings on female LRS. Nonetheless, in general, earlier age at first reproduction is associated with females producing more offspring over their lifetime in the population (see Supporting Information D, Hayward et al., 2014). Therefore, having an earlier reproductive onset could still potentially indicate an increased fitness (Supporting Information D). In line with this, in this population, elder sister presence in later life increased the younger sister's annual reproductive success (Lynch et al., 2019). However, further studies are needed to confirm that having an elder sister might improve female sister reproductive output by advancing the age of first reproduction without any survival costs.

How could sister presence lead to such benefits? Helpers, including elder sisters, may have two major effects on their recipients: (a) lightening the investment required by mothers and allowing them to reproduce again sooner or (b) adding to the mother's investment, allowing them to produce calves with a higher probability of survival (Crick, 1992; Emlen, 1995). In rare cases for elephants, allomothers, which can include elder sisters, can lactate to support mothers (Lee, 1987), and also contribute to feeding (Berliani et al., 2019; Rapaport & Haight, 1987). In addition, non-lactating females sometimes allow alien offspring to manipulate their nipple (Lee, 1987; Robinson & O'Brien, 1991; Tronick et al., 1987), suggesting that allo-nursing might have other functions than just lactation, for instance to calm a stressed juvenile (Lee, 1987; Plotnik & de Waal, 2014). Opportunities for social bonds with relatives may also be advantageous for younger female siblings. Previous studies on social mammals have found that long-lasting social bonds among females have beneficial effects on reproductive success and longevity (Russell et al., 2007; Silk, 2007; Sparkman et al., 2011). Among long-lived mammals, consistent social interactions are associated with numerous benefits (Kikusui et al., 2006; Silk, 2014), such as coalitional support, protection from harassment, greater access to resources or reduced vulnerability to predators, as well as health benefits

TABLE 4 Output of the retained models of focal calf short- and long-term survival by the model selection (see Table 1). We provide the estimates, SE, Z-value, *p*-value and *T*-value. For focal calf survival from 6 years old, *Log(scale)* corresponds to the logarithm of the estimated scale parameter. $\text{Log}(\text{scale}) = 0.28$ meaning that 1.32 is the standard deviation of the logarithm of survival time

Dependent variable	Estimate	SE	Z	<i>p</i>	<i>T</i>
Focal calf survival between 0 and 5 years old					
Intercept	-0.33	0.75	-0.44	0.66	—
Birth order	0.04	0.06	0.55	0.58	—
Censor	-2.48	0.13	-18.87	<0.01	—
Mother origin	-0.04	0.13	0.33	0.74	—
Birth interval: Long	0.04	0.09	0.43	0.67	—
Birth interval: Short	0.20	0.16	1.23	0.22	—
Focal calf survival from 6 years old					
Intercept	4.97	1.40	3.55	<0.01	—
Concurrent	0.49	0.18	2.70	<0.01	—
Focal sex	-0.67	0.17	-3.93	<0.01	—
Elder sex	-0.26	0.18	-1.44	0.15	—
Focal sex: Elder sex	0.51	0.24	2.10	0.04	—
Mother origin	-0.07	0.15	-0.50	0.62	—
Birth order	0.09	0.06	1.48	0.14	—
Mother age class (22–28)	-0.04	0.25	-0.17	0.86	—
Mother age class (29–37)	0.05	0.26	0.20	0.84	—
Mother age class (38+)	-0.02	0.29	-0.09	0.93	—
Cohort 1960	0.13	1.37	0.10	0.92	—
Cohort 1965	0.47	1.35	0.35	0.73	—
Cohort 1970	0.75	1.35	0.56	0.58	—
Cohort 1975	-0.15	1.35	-0.11	0.91	—
Cohort 1980	0.24	1.35	0.18	0.86	—
Cohort 1985	0.49	1.35	0.36	0.72	—
Cohort 1990	0.68	1.35	0.50	0.62	—
Cohort 1995	0.78	1.37	0.57	0.57	—
Cohort 2000	1.07	1.41	0.76	0.45	—
Cohort 2005	0.94	1.39	0.68	0.50	—
Region Chin_Shan	-0.90	0.28	-3.22	<0.01	—
Region Kachin	-0.52	0.49	-1.08	0.28	—
Region Magway_Mandalay_Naypyidaw	-0.71	0.21	-3.40	<0.01	—
Region Others	-1.48	0.49	-3.03	<0.01	—
Region Sagaing	-0.78	0.20	-3.82	<0.01	—
Birth interval: Long	-0.007	0.02	-0.38	0.71	—
Birth interval: Short	-0.10	0.05	-1.99	0.05	—
Log(scale)	0.28	0.06	4.78	<0.01	—

including positive effects on stress response systems, immune function and health (Silk, 2014). This hypothesis is supported by the fact that the presence of elder sibling (either sex) increased focal survival of both sexes from 6 years old. More generally, in social species characterized by cooperative behaviours, the presence of helpers (which are usually elder brothers and sisters of the family group) is associated with delayed senescence and increased longevity (Berger et al., 2018; Hammers et al., 2013), thus suggesting that elder siblings can influence life-history trajectories. Our findings suggest long-term benefits for females raised with elder sisters, which

complements studies reporting that close relationships between females within matriarch-led multi-generational herds (McComb et al., 2001) benefit offspring in the group (Lahdenperä et al., 2016; Lynch et al., 2019).

Conversely, we found that sibling effects can entail costs for subsequent offspring, in line with some previous findings (Bérubé et al., 1996; Rickard, 2008; Trillmich & Wolf, 2008). However, contrary to our expectations, we did not highlight important costs of elder brothers on the subsequent offspring. Instead, our results show that the elder sisters were costly for subsequent males in

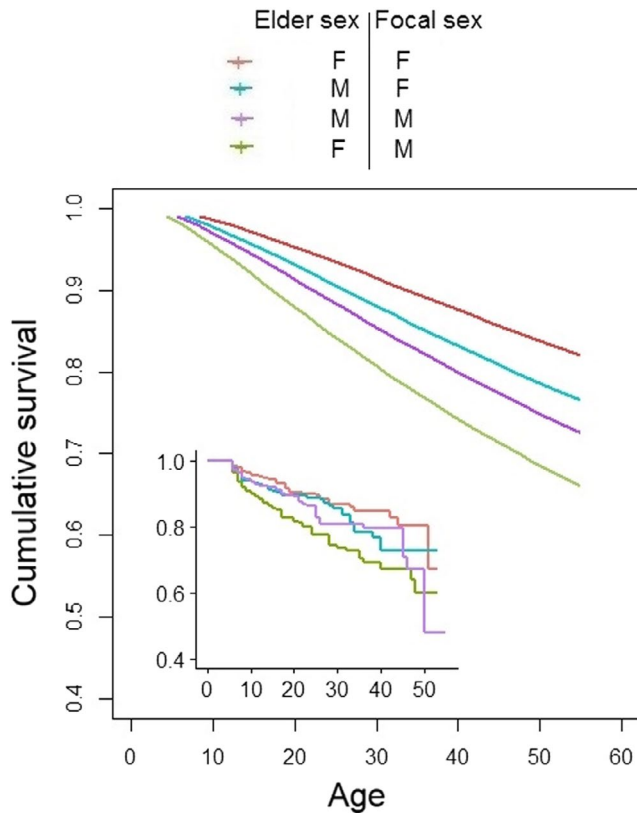


FIGURE 4 Cumulative survival curves for focal calves from 6 years old as a function of both elder and focal calf sexes from the best AFT model (including an interaction between the elder and focal calf sexes). We also provide the Kaplan–Meier fit on raw data (*survfit* function in the *SURVIVAL* package) on the inner panel

terms of survival. Nonetheless, males with elder sisters displayed reduced body mass when the siblings were not raised concurrently, whereas when the elder female was present, males displayed a weight advantage. Although our low sample size precludes from drawing any strong conclusions, detrimental effects of elder sisters may be explained by life-history trade-offs where the positive early-life effect of elder sisters on male body mass could lead to survival cost later in life. This is in line with the life-history theory which predicts a negative relationship between early-life growth and/or reproduction, and organism maintenance (Kirkwood & Rose, 1991). In such contexts, males could adopt the 'live-fast, die-young' strategy when raised with their elder sister. This hypothesis is consistent with other studies in mammals evidencing an effect of early-life conditions on life-history trade-offs (e.g. Hammers et al., 2013; Nussey et al., 2007). The two contrasted effects of elder sisters on their brothers might be driven by different mechanisms. The positive impact of elder sister's presence on subsequent males is probably attributed to the help and benefits that elder sisters provide when present. The negative effect of elder sisters when they were raised apart on younger male body mass could reflect a possible heterogeneity in maternal ability to care for offspring. However, we did not see any effect of maternal age nor interaction between elder

sibling sex and birth interval on any of the parameters measured in this population (Supporting Information C). This analysis indicated that after accounting for maternal age, reduced maternal allocation is unlikely to explain the negative effects we observe on siblings. In addition, we controlled for maternal reproductive history (parity) on the parameters measured, which did not affect our results. Evolutionarily, the positive effect of elder sisters on a morphological trait of brothers could be explained by kin selection shaping life histories (Bourke, 2007; Lucas & Keller, 2020); and more specifically by the fact that our study species is marked by a matrilineal social structure, where males in nature disperse at adolescence, and are less gregarious than females (Moss, 2001; Sukumar, 2003). Males might need to leave the natal family with a certain body condition that would guaranty their survival and reproductive success outside the social group. Unfortunately, we do not have access to males' reproductive traits to confirm the fitness outcomes for subsequent male siblings.

More generally, could our results be driven by differences in maternal allocation between sexes? Elder brothers may have detrimental effects on siblings because mothers producing a son in the previous reproductive event incurred a greater reproductive cost, which rendered them less able to allocate in future reproductive events. In mammals, considerable evidence across mammals, including Asian elephants, shows that producing sons versus daughters is indeed more costly to mothers (see Rickard et al., 2007). Our results could thus reflect a possible heterogeneity in maternal quality so that 'better' mothers have shorter interbirth interval and possibly higher calf survival, and also produced heavier offspring. However, we think that is unlikely, first, because the results gained from the analyses including the interaction between birth interval and elder sex on each subsequent calf life-history trait provided no evidence for this hypothesis. Second, previous results in our study population indicating that shorter interbirth intervals negatively correlate with calves' survival (Mar et al., 2012) do not either support this hypothesis. Still, we were not able to fully disentangle sibling effects from maternal allocation, and therefore it is possible that differences in maternal quality rather than direct sibling interactions partly explain our results.

Contrary to our expectations, sibling sex and/or presence did not influence variation in all focal calf life-history traits we tested. Indeed, we did not detect any sibling effects for some of the focal calf traits. First, elder sibling sex or presence did not influence focal calf sex (prediction 1). Offspring of the larger sex, typically males, require more resources, and many studies have explored how the elder sex affect subsequent offspring sex (Bérubé et al., 1996; Clutton-Brock et al., 1981; Helle et al., 2002). For instance, in big-horn sheep *O. canadensis*, the year after weaning (the more costly) sons, ewes were more likely to have a daughter than a son if in poor condition (Douhard et al., 2016). Our result could thus suggest that producing a male or a female was not more costly for mothers in their living environment. Second, we did not evidence the effect of the elder sibling presence or sex on the focal calf survival to 5 years old. Here, the effect of elder sibling sex on mortality risk depends on the life stage. Indeed, although there was no effect of elder sibling

sex on subsequent offspring early life survival (to 5 years), it had an effect later in life (i.e. after weaning). Consequently, similarly to humans (Nitsch et al., 2013), our results highlight that siblings can have heterogeneous effects on each other's life-history traits at different life stages, in line with previous results in our population (Lynch et al., 2019), thus suggesting that optimal trade-offs between cooperation and competition between siblings could vary across an individual's life span.

In summary, we present clear evidence of long-term sibling effects in a long-lived non-human species. Overall, our results highlight heterogeneous effects driven by the sex of the elder sibling, with overall positive effects of having an elder sister in Asian elephants and less strong effect of elder brothers on subsequent siblings. Therefore, the sex of elder siblings could have a significant influence on the life trajectories of subsequent offspring, with differential effects of the sex of elder siblings implying sex-specific helping behaviour and/or sex-specific competition. Because the current study is on semi-captive individuals that are subject to workloads and management, calves are separated from mothers at the ages of 4–5. However, even if siblings do not necessarily associate after weaning, the long-term effects we observe are very likely to be the downstream effects of early-life conditions (e.g. Berger et al., 2018; Hammers et al., 2013; Monaghan et al., 2011; Russell et al., 2007; Sparkman et al., 2011). Our results therefore highlight the importance of taking all life stages into consideration when evaluating sex allocation effects on life trajectories, and that effects can be trait-dependent. Finally, even if the underlying mechanisms are unknown, our findings entail implications for calculations of maternal fitness and for considering the selective pressures and ecological constraints relevant to the evolution of sex-ratio adjustment.

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COMPETING INTERESTS

The authors declare no competing financial interests.

AUTHORS' CONTRIBUTIONS

V.B., S.R., M.L. and V.L. designed the study; W.H. collected the data; V.B., M.L. and J.J. analysed the data, with contributions from S.R.; V.B. and S.R. wrote the paper with contributions from M.L., J.J., W.H. and V.L. All authors provided editorial advice and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4j0zpc8bv> (Berger et al., 2021).

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SUPPORTING INFORMATION

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

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