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1 TITLE

2 Evolutionary significance of maternal kinship in a long-lived mammal

3

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13 SUMMARY

14 Preferential treatment of kin is widespread across social species and is considered a central prerequisite to
15 the evolution of cooperation through kin selection. Though it is well known that, among most social mammals,
16 females will remain within their natal group and often bias social behavior towards female maternal kin, less is
17 known about the fitness consequences of these relationships. We test the fitness benefits of living with maternal
18 sisters, measured by age-specific female reproduction, using an unusually large database of a semi-captive Asian
19 elephant (*Elephas maximus*) population. This study system is particularly valuable to an exploration of reproductive
20 trends in a long-lived mammal because it includes life-history data that span multiple generations, enabling a study
21 of the effects of kinship across a female's lifespan. We find that living near a sister significantly increased the
22 likelihood of annual reproduction among young female elephants, and this effect was strongest when living near a
23 sister 0 to 5 years younger. Our results show that fitness benefits gained from relationships with kin are age-specific,
24 establishes the basis necessary for the formation and maintenance of close social relationships with female kin, and
25 highlights the adaptive importance of matriliney in a long-lived mammal.

26

27 Keywords: kinship, Asian elephant, fertility, matriliney

28 INTRODUCTION

29 Among social mammals, there is widespread evidence that individuals prefer kin over nonkin as social partners
30 [1–3]. Generally, these preferences are explained by kin selection theory [4], whereby kin-biased cooperation and
31 affiliation is predicted when the inclusive fitness benefits (direct fitness via an individual's own reproduction and
32 indirect fitness via the reproduction of relatives) outweigh the costs of these behaviors. In particular, within
33 matrilineal societies, where females remain in their natal group and males disperse [5,6], females may live in the

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34 same social group throughout their lives and are therefore expected to bias altruistic behaviors towards close
35 maternal relatives [1,7]. Empirical observations support these predictions and indicate that most female mammals
36 maintain closer proximity and spatial associations with female maternal kin, suggesting female-biased kinship
37 serves an important adaptive function (see reviews [1,2]).

38 The most complete information on the measurable fitness consequences of female kinship come from studies
39 on small, short-lived mammals, which show that the presence of maternal kin enhances female reproduction (see
40 review [2]). For example, in house mice (*Mus domesticus*), females housed with sisters experienced shorter
41 interbirth intervals and produced more offspring per litter with greater overall weight, than those housed with nonkin
42 [8]. Among Kalahari meerkats (*Suricata suricatta*), offspring weight and survival were directly related to the
43 number of maternal kin present [9]. Such studies confirm the reproductive benefits that may be gained through
44 associating with female relatives among short-lived mammals.

45 When examining the evolutionary consequences of female-biased kinship, however, it is crucial to distinguish
46 between the selection pressures experienced by short- and long-lived mammals. Life-history differences may have
47 significant implications on the adaptive function of kin-biased behaviors. Compared to short-lived species, long-
48 lived mammals experience longer generation times, slower rates of reproduction [10], and suffer from senescence
49 in survival at a relatively younger age [11]. These different life-histories may be linked to different reproduction
50 and survival strategies that must be flexibly utilized across a long lifespan. For example, because long-lived
51 mammals are characterized by prolonged periods of immaturity [10], females are particularly dependent upon the
52 help of relatives. As such, additional investment in youngsters from nonmothers may play a particularly important
53 role in long-lived species, where extra help may enhance the development of immatures [12,13] and lead to higher
54 reproductive success of mothers [12]. It is therefore important to examine the evolutionary consequences of kinship
55 in long-lived mammals to broaden our understanding of the adaptive function of female-biased kinship.

56 Little research has addressed the fitness benefits associated with maternal kinship in long-lived mammals,
57 however. This basic gap in our knowledge is primarily due to the difficulty of recording the required breadth of
58 information, across multiple generations that is needed to comprehensively analyze the proximate and ultimate
59 effects of kinship. Of the few studies that have been able to access longitudinal records of wild or free-ranging long-
60 lived mammals, powerful empirical evidence highlights the need to further explore the evolutionary significance of
61 maternal relatives; particularly, that associating with maternal relatives increases care for dependent young [14,15]
62 while also decreasing infant mortality [16,17]. More generally, the presence of close female maternal kin (mothers
63 and sisters) has been found to significantly improve female reproductive success (nonhuman primates: [18–20];
64 cetaceans: [21,22]; elephants: [12,23]). These results parallel those from human studies, which show that female
65 reproductive success improves with help from mothers and pre-reproductive daughters [24–26].

66 There are several possible mechanisms driving such improved reproduction when living near maternal
67 relatives. In long-lived mammals, consistent social interactions have been shown to have significant affects (positive
68 or negative) across a range of traits, from physiological (e.g. body condition, stress) to social (e.g. social
69 status)[2,3,27,28]. It is therefore possible the presence (or absence) of kin, as social partners [1,2], may have direct

70 effects on a female's health and, consequently, her lifetime reproduction success. For example, a study of wild
71 African elephant (*Loxodonta africana*) herds disturbed by poaching found that females had higher fecal
72 glucocorticoid concentrations (indicative of stress) and lower reproductive output when living in herds with
73 unrelated conspecifics, as compared to females living with relatives [29]. In addition, positive associations with
74 relatives may shorten a female's inter-birth interval by decreasing her required investment in offspring [30],
75 resulting in earlier weaning and earlier re-start of reproductive cycling [31].

76 While these studies have made important contributions to our understanding of the adaptive value of female-
77 biased kinship, three notable shortcomings constrain interpretations about the evolutionary trends of matriliney. First,
78 studies on wild populations are unable to tease apart the cause and effect of the presence of kin. Large families will
79 be able to maintain access to large areas of resources *and* have access to a large number of potential helpers, all of
80 which may contribute to a female's reproductive success. Our understanding of the adaptive consequences of
81 kinship would therefore benefit from the ability to control for such confounding factors, such as family size and
82 resource availability across different locations, in a species' native environment.

83 Second, previous work has done little to address the effects of maternal relatives on reproductive success across
84 different stages of life in long-lived mammals, despite the changing needs of individuals as they age. For example,
85 because primiparous females experience a greater risk of pregnancy loss/stillbirth [32] and offspring mortality [32–
86 34], young, inexperienced females may benefit more from supporting kin networks than their older, experienced
87 conspecifics. It is therefore possible that the fitness benefits accrued by living near kin are age-specific, changing
88 over an individual's lifespan, but this has yet to be thoroughly studied (but see [12,35,36]).

89 Finally, the age of the maternal relative should be considered, yet few studies have considered how optimal
90 strategies for an individual may change over time (but see [35,37,38]). A careful analysis of these strategies requires
91 an examination of siblings over different life stages, which will enable an examination of how an individual may
92 alter their behavior across their lifespan towards the same relative. Explanations of the evolution of non-parental
93 investment in social mammals include two, non-mutually exclusive hypotheses for how kin may maximize their
94 fitness. One explanation posits that assisting in the care of young may yield direct benefits by providing experience
95 that enables them to become more successful parents [39–42]. In this interpretation, younger, inexperienced females
96 gain future reproductive benefits through helping older sisters. A second hypothesis focuses on indirect fitness
97 benefits, theorizing that females may assist the reproductive efforts of sisters if it significantly improves sister
98 reproductive success [4,30]. Here, it is possible that older females may gain indirect fitness benefits through helping
99 a younger, more fertile sister when she is not investing in her own reproductive efforts. Alternatively, if resources
100 are limited, an older sibling with more experience might benefit more from investing in her own reproductive efforts
101 than those of a younger sister [30]. Indeed, though females may experience differing selective pressures to invest
102 in a sibling's reproductive efforts across different life stages, the consequences of these strategies remain largely
103 unknown.

104 Here, we investigate the reproductive effects of living near maternal sisters across a female's lifetime in semi-
105 captive Asian elephants (*Elephas maximus*). The majority of work, to date, on the effects of relatives on female

106 fitness have focused on short-term measures, such as individual offspring growth, condition, or survival to breeding
107 age [2]. Consequently, potential effects of relatives on other fitness outcomes, such as annual reproductive output
108 across an individuals' lifespan, are not well studied, despite their key importance to a female's lifetime reproductive
109 success. This is particularly true for long-lived mammals which reproduce at a comparatively slower rate [10]. We
110 focus our analysis on maternal sisters for two reasons. First, building on previous work demonstrating the
111 importance of mothers on female reproduction in Asian elephants [12], we seek to expand our understanding of the
112 impact of maternal relatives to sisters. Second, a focus on siblings enables a comparative exploration of the potential
113 benefits or costs of living near maternal relatives across different ages (i.e. older and younger than the focal
114 individual), while holding the type of relatedness constant.

115 Our study population of elephants offers a particularly ideal opportunity to effectively address such questions
116 about the adaptive effects of female-biased kinship on reproduction. Asian elephant females live within multi-
117 generational, matriloca herds [14], which may facilitate the evolution of nepotistic behaviors among female kin. In
118 addition, their long lifespans enable the development of complex and enduring social relationships among female
119 relatives and provide an opportunity to explore the age-specific effects of living near kin. Because elephants, like
120 other long-lived mammals, are characterized by extended periods of immaturity [10], additional investment from
121 female kin may play a particularly important role in these social systems. As such, elephants may provide a useful
122 comparison to other long-lived, social mammalian species, to illuminate the evolutionary mechanisms of female-
123 biased kinship.

124 We use one of the world's largest, most comprehensive dataset on semi-captive Asian elephants, employed in
125 the timber logging industry, to examine the relationship between maternal kinship and reproductive success in a
126 long-lived mammal. This longitudinal dataset, generated by the Myanma Timber Enterprise (MTE), includes
127 comprehensive demographic information tracked across several generations, enabling a study of fitness benefits
128 over a female's lifetime. We are therefore able to conduct a time-event analysis to investigate the association
129 between a female's annual reproductive output and: 1) the presence of a maternal sister; and 2) sister age difference.
130 For both analyses, we also consider age-specific effects to explore the importance of maternal relatives across a
131 female's lifetime. Second, a particularly valuable feature of this population is that we may test questions related to
132 kinship while teasing apart critical environmental influences due the unique conditions of the population. While
133 these semi-captive elephants live within their natural habitat and experience natural birth and death rates, unlike
134 their captive counterparts [43], the elephants are employed for sustainable forestry work. Depending on MTE's
135 timber harvesting needs, family members are either kept in their original natal group or relocated. These conditions
136 present a "natural experiment" where some individuals continue to live near relatives while others live without kin.
137 In this way, we may avoid the confounding influence of factors on female reproductive success, such as group size,
138 location and inherent differences in mortality and genetic quality. We aim to gain insight into the possible selective
139 pressures driving female-biased kinship in a long-lived, social mammal.

140
141 METHODS

142 *Study Population*

143 The timber camps of Myanmar contain the world's largest (N~5,000) remaining semi-captive population of
144 elephants [44]. For over a century, the Extraction Department, Myanma Timber Enterprise, has kept records of each
145 animal's permanently marked identification (ID) number and name, origin (wild-caught or captive-born), date and
146 place of birth, mother's ID number and name, age or year of taming, birth dates and ID numbers of all offspring,
147 date of death or last known date alive and cause of death.

148 The elephants live within their native forest habitat, distributed across the country and are used during the day
149 as riding, transport and draft animals, following strict set working hours, working days per year, and tonnage per
150 individual. During the night, however, the elephants forage in the forest, unsupervised, and may interact and mate
151 with both wild and tame conspecifics. Breeding rates are natural (without human intervention), and calves are cared
152 for and nursed by the biological mother until lactation no longer supports their demands (~ age 4). Calves are then
153 separated from the mother and tamed, after which they may return to their natal group or may be relocated,
154 depending upon timber harvesting needs.

155 *The Sample*

156 This study includes 475 captive-born females, born since 1959 and survived to at least age 12 (marking the
157 beginning of a female's true reproductive career). No twins were included in this study. Maternal siblings were
158 determined by shared mother ID and only sisters over the age of 5 were considered in the analysis: before this age,
159 individuals are still nursing and dependent on their mothers.

160 The timber landscape is composed of many townships where different logging camps and working groups
161 reside. Based on the ability of the elephants to roam and interact with conspecifics during their free time, relatives
162 living in the same township were considered to be "near" one another whereas those living in disparate townships
163 were considered "far"; those living within the same township are more likely to have the opportunity to engage in
164 affiliative behaviors outside working hours compared to those living in different townships. Ultimately, the analysis
165 included individuals from 30 townships across the entire country.

166 *Statistical Analysis*

167 All analyses were conducted with R (version 3.4.4).

168

169 *1. Does the presence of a maternal sister have an age-specific effect on female reproduction?*

170 We studied age-specific effects of sister presence on female age-specific reproductive rate by focusing our
171 analysis on three separate life stages. Age-specific fertility in female elephants generally shows a U-shape curve,
172 as seen in humans [45]. However, Hayward et al. [46] and Lahdenperä et al. (in preparation) found that this curve
173 of age-specific reproductive probability follows a "life stages" pattern in the population: low annual breeding
174 success at ages 5-11; a rapid increase between ages 12-21; little change from age 22-43; and a steep decline from
175 44 onwards. Because reproduction is so distinct between life stages, a model including all ages and treating age as
176 a linear, quadratic or higher order polynomial term provides worse model fit[46] than when cutting analyses

177 according to these different life stages and treating age as linear within these age groups. Therefore, our analysis
178 focused on the latter three stages, due to our interest in breeding success rates.

179 Because sibling presence is not constant throughout a female's lifetime, we used discrete time-event analysis,
180 with constant and time varying variables at each year of a females' life. As such, annual breeding success was the
181 dependent variable (binary: 0=did not produce a calf in the given year; 1=produced at least one calf), and analyzed
182 using binomial generalized linear mixed-effect models (GLMMs) with a logit-link function through the "glmer"
183 function in the "lme4" package [47]. The main term of interest was sibling presence (time-varying: 0=no female
184 sibling living within the same township that year, 1=at least one female sibling present in the same township that
185 year). We chose a binomial approach over continuous number of sisters because few females had more than one
186 sibling present at a given time. We controlled for the following variables, known to potentially influence female
187 reproductive rates, as fixed effects: mother living status [12] (time-varying, categorical: 0=mother alive, 1=mother
188 dead, 2=mother's status unknown), mother origin [45](0=wild-born, 1= captive-born), female birth order [45](0=not
189 first born, 1=first-born or only born). In addition, we included linear term for female age (time-varying, continuous)
190 based on previous work on age-specific reproduction in female elephants in this population [46]. To improve model
191 convergence and interpretation, age was re-scaled to 0-40 (i.e., where the youngest age included in the data (here,
192 age 12) was labeled "0" and the oldest age (here, age 50) was labelled "40". An interaction term, sister
193 nearby*female age, was also included as a fixed effect term to explore whether the effect of a sister's presence
194 changes with female age. Including this interaction term allowed us to evaluate the effects of not only sister
195 presence, but also reveal possible disproportionate effects of such a presence on female reproduction across a life-
196 stage.

197 To adjust for any temporal or spatial variation in birth and death rates across Myanmar, we included "year"
198 (N=60) and "ecological division" (N=4) as random terms. The logging townships were divided into 4 larger areas
199 representing different ecological landscapes, based on elevation meters from sea level: coastal, central,
200 mountainous, and northern, using topological data provided by Myanmar Information Management Unit (Map ID:
201 MIMU001, 2007). Finally, we included mother ID as a random term to adjust for genetic and maternal effects (e.g.
202 inherited fitness; N=336) between maternal sisters.

203 For each life stage, we followed the same statistical methods, using the same fixed and random effects.
204 However, for the oldest life stage, because the variance and standard deviation for all random effects (year, Mother
205 ID, and ecological division) were null (likely due to the small sample size of this age group), we used binomial
206 generalized linear models (GLMs) with a logit-link function without random terms, as opposed to GLMMs. Also,
207 due to the extreme discrepancy between the number of females living with and without a sister nearby in the oldest
208 female age group, we were unable to include squared age and the interaction term of female sibling nearby*female
209 linear age. Instead, both terms were included as separate main effects only.

210 Female age and sister nearby variables were kept in the final models as they were the variables of main interest
211 in the models. All other fixed terms were retained in models only if they improved explanatory power, determined
212 using Akaike Information Criteria (AIC)[48]. To do this, we used the drop1() function in R to examine each

213 individual fixed effect, where a likelihood ratio test was conducted between the full model and a model without a
214 particular variable (i.e. “single term deletions”). To obtain odds ratios (OR) instead of coefficients on the logit scale,
215 the regression coefficients and the 95% confidence intervals (CI) were exponentiated for each final model of
216 interest.

217 We first tested whether young, inexperienced females (ages 12-21, N=475) are more likely to reproduce when
218 living near a maternal sister. Within this subset, there were 4,373 observation years (not near a sister, N=3,232; near
219 a sister, N=1,141), with 244 births, where each female’s reproductive output during the observation period ranged
220 from 0-4 calves (mean 0.41 ± 0.69). For each year during this life stage, 0-4 maternal sisters lived nearby (mean
221 0.26 ± 0.59).

222 We then investigated the reproductive effects of living near a sister in middle aged females (N=391, ages 22-
223 43). This subset contained 4,878 observation years (not near a sister, N=3,806; near a sister, N=1,072), with 404
224 births, where each female’s reproductive output ranged from 0-7 calves (mean 1.04 ± 1.3). For each year during
225 this life stage, 0-4 maternal sisters lived nearby (mean 0.21 ± 0.55).

226 Finally, we examined the reproductive effects of living near a sister in the oldest age group of females (N=89,
227 ages 44-50). This subset contained 407 observation years (not near a sister, N=353; near a sister, N=54), with 22
228 births, where each female’s reproductive output ranged from 0-2 calves (mean 0.26 ± 0.55). For this stage of life,
229 0-2 maternal sisters lived nearby, annually (mean 0.08 ± 0.31).

230

231 *2. Does the age difference between sisters have an age specific effect on female reproduction?*

232 We next tested for the effect of sibling age difference on female reproduction. This was carried out in a separate
233 analysis to above, because we here consider only females who lived near at least one sister at some point in their
234 lifetime (N=151, ages 12-50). We again examine age-specific effects on female reproduction by focusing our
235 analyses on separate life stages (young females, aged 12-21; middle aged females, aged 22-43). It should be noted
236 we were unable to examine the older female group (ages 44-50) due to the previously noted small sample size. Like
237 the previous models, we included mother ID as a random effect, necessitating the use of a GLMM. However, we
238 were unable to include the random effects of year and division due to smaller sample size. We considered the same
239 fixed effects as in the previous models but instead of the interaction term sister nearby*female age, we included
240 interactions between female age and each sibling age difference variable to test the reproductive effects of a
241 particular sibling changes with focal female age. Again, we used this interaction to explore the age-specific
242 reproductive effects of sibling age difference. Female age was kept in the final models but other terms were retained
243 in models only if they improved explanatory power, determined using Akaike Information Criteria (AIC)[48].

244 We first tested if young females (N=151, ages 12-21) were more likely to reproduce when living near a sister
245 of a particular age difference. Within this subset, there were 1,376 observation years, with 89 births, where each
246 female’s reproductive output ranged from 0-3 calves (mean 0.37 ± 0.68). For each year during this life stage, 0-4
247 maternal sisters lived nearby (mean 1.04 ± 0.7). Sibling ages were categorized: older sisters (by observation years:

248 0-5 years (N=258), 6-10 years (N=251), 11-15 years (N=125)) and younger sisters (by observation years: 0-5 years
249 (N=303), 6-10 years (N=301), 11-15 years (N=111)).

250 We then tested the effect of sibling age difference on reproduction in middle-aged females (N=118, ages 22-
251 43). Within this subset, there were a total of 1,316 observation years, with 119 births, where each female's
252 reproductive output ranged from 0-5 calves (mean 0.65 ± 1.1). For each year during this life stage, 0-4 maternal
253 sisters lived nearby (mean 1.02 ± 0.74). Sibling ages were again categorized: older sisters (by observation years: 0-
254 5 years (N=173), 6-10 years (N=154), 11-15 years (N=46)) and younger sisters (by observation years: 0-5 years
255 (N=246), 6-10 years (N=335), 11-15 years (N=218)).

256

257 RESULTS

258 *1. Does the presence of a maternal sister have an age-specific effect on female reproduction?*

259 We found that a sister's presence significantly increased a young female's (ages 12-21) annual chances of
260 reproduction, but, notably, the interaction between sibling presence and age had a significant negative effect (Table
261 1). For example, for a female at age 13, the chances of reproducing increased from 1% to 3% when a sister was
262 nearby. In contrast, a 19 year old female only increased her annual chances of reproduction in a given year by 0.06%
263 when living near a sister (Figure 1). Having a living mother also increased the chances to reproduce (Table 1).
264 These results were not confounded by year ($S^2=0.07\pm 0.27$), location ($S^2=0.053\pm 0.23$), mother identity
265 ($S^2=0.71\pm 0.84$) or other non-significant terms that were controlled for.

266 We found that only maternal living status was able to significantly predict annual female reproduction among
267 middle-aged females (ages 22-43), with those females with living mothers having increased annual chances of
268 reproduction compared to those whose mother was already deceased (Table 2). Middle-aged females were
269 characterized by a constant probability of reproduction, without age-dependent effects, and we did not find that a
270 sister's presence had a significant effect on the probability of annual female reproduction although the probability
271 of reproducing was higher when the sister was nearby (OR: 1.29, CI: 0.86, 1.93; Figure 1). These results were not
272 confounded by year ($S^2=0.09\pm 0.31$), location ($S^2=0.05\pm 0.22$), mother identity ($S^2=0.22\pm 0.47$) or other non-
273 significant terms that were controlled for.

274 In older females (ages 44-50) the probability of reproduction decreased clearly with age but sister presence,
275 mother's living status, birth order, and mother origin terms were non-significant (Table 3, Figure 1).

276

277 *2. Does the age difference between sisters have an age specific effect on female reproduction?*

278 Here we found that a sister 0 to 5 years younger living nearby significantly improved the likelihood of annual
279 reproduction of young, inexperienced females (Table 4, Figure 2) and that effect on younger females diminished
280 with age. For example, the chances of reproduction for a female at age 14 increased from 2% to 8% when a sister
281 0 to 5 years younger is nearby. On the other hand, a female at age 17 only increased her chances of reproduction by
282 2% when living near a sister 0 to 5 years younger. These results were not confounded by mother identity
283 ($S^2=0.44\pm 0.67$) or other non-significant terms that were controlled for.

284 We did not find any of our predictor terms to have a significant effect on middle-aged female reproduction
285 (Table 5).

286

287 DISCUSSION

288 Though it is well-established that relationships with relatives are a fundamental and universal aspect of
289 mammalian sociality [1], less is known about the long-term fitness consequences of female-biased kinship,
290 particularly among long-lived mammals [2]. Here, we measured the effects of maternal sister presence on female
291 reproduction across a lifespan in a semi-captive population of Asian elephants. We report that living near a sister
292 significantly increased the likelihood of annual female elephant reproduction among young individuals (ages 12-
293 21). Upon further exploration of this effect, we found that living near a sister 0 to 5 years younger is associated with
294 a higher likelihood of young female reproduction. These findings have implications for our understanding of the
295 fitness consequences of relationships with female relatives, as well as the selective pressures driving these social
296 bonds.

297 The presence of a maternal sister was positively and significantly associated with annual female
298 reproduction. Several mechanisms may be driving this difference in birth rates across individuals. For instance,
299 because pregnancy failures are common among Asian elephants, [32] it is possible that a sisters' presence may
300 protect a female from potential stressors that trigger such losses. Indeed, among long-lived mammals, consistent
301 social interactions are associated with numerous health benefits (see review by Silk and Kikusui et al. [3,27]) and
302 close kin are often preferred social partners [1,2]. The loss of such relatives is associated with stress and negative
303 health effects [49]. Among wild African elephants, for example, sociality is associated with improved body
304 condition [28,50] and kinship is a strong predictor of female social relationships [51]. Similar findings have been
305 reported in humans: greater social integration is associated with reduced mortality and better physical and mental
306 health [27], particularly for women [52]. In their study on the effects of mother presence on human female
307 reproduction, Lahdenperä et al. [24] found that females not only experience higher reproductive output when living
308 near their mothers, but also produced more offspring throughout her lifetime, and with higher survival rates.
309 Considering the numerous benefits that may be gained through social ties with female kin across mammalian
310 species, the ability to associate with a maternal sister may therefore have positive effects on female fertility and
311 reproduction in Asian elephants.

312 It should be noted, however, that we found an age-specific effect throughout our analyses where young females
313 were more likely than their older conspecifics to reproduce within a given year when living near a sister. While the
314 proximate mechanism driving enhanced reproduction may be related to improved health generated by sociality
315 [3,27], such disproportional benefits accrued across a lifespan may also be the result of two age-specific biological
316 and behavioral phenomena. First, young females often have fewer bodily resources available for mobilization
317 during pregnancy and lactation [53], perhaps due to the trade-offs faced by such youngsters between allocating
318 energy to reproduction or their own continued development [54]. This paradox is exacerbated by an extended period
319 of immature development, which significantly increases the energetic burden placed on a mother [10]; females in

320 our population gain height on average until age 15 and weight until age 35 [55]. Second, parenting experience may
321 be critical to successfully rear offspring [39–42], positioning young, inexperienced females at a disadvantage.
322 Indeed, offspring of young, inexperienced females often experience greater mortality [32–34]; assistance from
323 relatives may therefore be particularly valuable to young females. Similar results to the ones reported here have
324 been found among Asian elephants, where a maternal grandmothers' presence is associated with improved grand
325 calf survival and increased reproductive output of the daughter, and this effect was particularly strong among young
326 females [12]. The combined theoretical and empirical support presented here suggest both experience and energetic
327 demands may play an important role in mediating relationships with female maternal relatives, particularly early in
328 female reproductive career.

329 We also found that the presence of a sibling 0 to 5 years younger is associated with a higher likelihood of
330 female reproduction. This result may be interpreted through an understanding of common explanations of
331 alloparental care, often where behavioral decisions may be simplified to assisting the reproductive efforts of
332 relatives versus seeking direct fitness benefits via reproductive opportunities [30]. In our analysis, the grouping of
333 sisters 0 to 5 years younger than the “young female group” ranged in age from 7 to 16, whereas peak probability
334 of reproduction is seen among females aged 18 to 22. Because these younger sisters are not within the age range
335 of peak reproduction, rather than risk seeking out breeding opportunities themselves, they may benefit more
336 through assisting the reproductive efforts of their older sisters by promoting their annual reproductive output, and
337 perhaps ultimately gaining both parenting experience and indirect fitness benefits through helping related infants
338 [39–42]. Alternatively, a maternal effect may generate these results, whereby females with shorter inter-birth
339 intervals are in better condition and have daughters with relatively higher reproductive output. This is unlikely,
340 though, because we only see an effect of younger siblings on young female annual reproductive probability,
341 whereas a maternal effect would predict a high reproductive output across a female's reproductive career. We
342 would expect similar effect in the presence of 0-5 years older siblings, but this was not found. Furthermore, we
343 include mother ID as a random effect to help control for such heritable differences.

344 While it is also possible that older sisters may gain indirect fitness benefits from promoting their younger sister
345 reproduction, we did not find any evidence of this effect in our study. These results may be explained by competition
346 between two potentially reproductive females. If resources are limited, for example, an older sibling with more
347 experience might invest more in her own reproductive efforts than those of a younger sister [30]. Alternatively,
348 though older sisters may not promote annual female reproduction, they may provide investment in other ways not
349 measured here, such as direct care for the offspring. Nonetheless, our findings establish that sibling effects on female
350 fertility are not uniform over time, but, rather, differ across an individual's lifespan.

351 Some caveats must be noted when interpreting these results. First, females in these groups live near other types
352 of kin and non-kin, which may also contribute to their reproduction. In social mammals, while mothers and sisters
353 are generally considered preferred social partners [1,2], other maternal relatives may also serve as allies in these
354 groups, such as aunts and cousins. Generally, however, such categories of kin are considered “distant relatives” and
355 are not typically associated with the fitness benefits gained through social integration [2,7]. Second, our location

356 data does not consider the potential for multiple transfers of the focal female or her sister, and mainly lists the first
357 allocated working location of a given individual. However, this would most likely under-estimate (and not over-
358 estimate) the effects of sisters on female reproductive rate by causing greater variation in the dataset and weaker
359 statistical significance (e.g. among middle-aged females where clear positive effects of sisters were visible).
360 Furthermore, we are still able to conclude that females living with and without sisters experience different annual
361 rates of reproduction, despite not knowing the specific transfer patterns.

362 Our study demonstrates the adaptive value of female-biased kinship in a long-lived species and provide support
363 to a greater body of knowledge, suggesting that social bonds with female maternal relatives improve female fertility
364 and fitness. In humans, general sociality is tied to enhanced physical and mental health [45], and this effect is
365 particularly strong among females [52]. Furthermore, human female reproductive success significantly improves
366 with help from close female maternal kin, such as mothers and pre-reproductive daughters [24–26]. Our results
367 build on these findings, showing that fitness benefits gained from relationships with kin are age-specific for both
368 the female and her relatives in Asian elephants. It is therefore possible that, among long-lived mammals, the
369 selective pressures for female-biased kinship change across an individual’s lifespan, where the motivation to nurture
370 social bonds with female relatives are age-dependent, resulting in different fitness benefits. Overall, this study
371 establishes a basis necessary for the formation and maintenance of close social relationships with female kin among
372 social, long-lived mammals.

373

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379 Robert Lynch for their assistance with data formatting, analysis, and graphic composition.

380 ETHICS

381 There are no ethical issues related to the demographic data on Asian elephants because it is collected from historical
382 records and no experimental protocols were used in collecting the dataset.

383 DATA ACCESSIBILITY

384 The data used for this analysis is property of the Myanmar Government. While we are unable to authorize public
385 use of the data, specific requests for re-analysis purposes may be directed to V.L. The materials supporting this
386 article have been uploaded as part of the supplementary material.

387 AUTHORS’ CONTRIBUTIONS

388 E.C.L, V.L., and M.L. conceived and designed the paper. E.C.L. performed all analyses and wrote the paper with
389 contributions from all authors. All authors read and approved the final manuscript.

390 COMPETING INTERESTS

391 The authors declare no competing financial interests.

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395

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507 **Table 1: Time-event model of maternal sister presence on young female reproduction (ages 12-21) in Asian**
508 **elephants.** Terms retained and rejected in the final model (determined using AIC) are shown above and below the
509 intercept, respectively. Mother's identity, year, and location were fitted as random terms.
510

Term	Estimate	Standard Error	Z value	P value
Sister nearby (0=far)	0.8	0.33	2.35	<0.05
Female age	0.23	0.03	7.6	<0.001
Mother's living status (0=alive)	-0.39	0.19	-2.02	<0.05
Sister nearby*Female age	-0.1	0.05	-1.93	<0.05
Intercept of Full Model	-4.29	0.25	-17.22	<0.001
Birth order (0=not first born)	0.2	0.18	1.03	0.3
Mother's origin (0=wild born)	-0.2	0.19	-1.06	0.29

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513 **Table 2: Time-event model of maternal sister presence on middle-aged female reproduction (ages 22-43) in**
514 **Asian elephants.** Terms retained and rejected in the final model (determined using AIC) are shown above and
515 below the intercept, respectively.

Term	Estimate	Standard Error	Z value	P value
Sister nearby (0=far)	0.21	0.15	1.42	0.15
Mother's living status (0=alive)	-0.25	0.12	-1.98	<0.05
Female age	-0.01	0.01	-1.56	0.12
Intercept of Full Model	-2.5	0.2	-12.29	<0.001
Sister nearby*Female age	0.004	0.02	0.21	0.83
Birth order (0=not first born)	-0.14	0.13	-1.02	0.31
Mother's origin (0=wild born)	0.11	0.13	0.87	0.39

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524 **Table 3: Time-event model of maternal sister presence on older female reproduction (ages 44-50) in Asian**
 525 **elephants.** Terms retained and rejected in the final model (determined using AIC) are shown above and below the
 526 intercept, respectively.
 527

Term	Estimate	Standard Error	Z value	P value
Female age	-0.3	0.14	-2.14	<0.05
Sister nearby (0=far)	-1.3	1.04	-1.21	0.22
Intercept of Full Model	-3.36	1.1	-3.04	<0.01
Mother's living status (0=dead)	1.14	1.08	1.06	0.3
Birth order (0=not first born)	-0.02	0.52	-0.05	0.96
Mother's origin (0=wild born)	0.79	0.53	1.5	0.14

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530 **Table 4: Time-event model of maternal sister age difference on young female reproduction (ages 12-21) in**
 531 **Asian elephants.** Terms retained and rejected in the final model (determined using AIC) are shown above and
 532 below the intercept, respectively. Mother's identity was fitted as a random term.
 533

Term	Estimate	Standard Error	Z value	P value
Female age	0.17	0.04	3.65	<0.001
Female age*Age difference: 0 - 5 years younger	-0.16	0.08	-1.92	0.05
Age difference: 0-5 years younger	1.4	0.47	3.03	<0.001
Intercept of Full Model	-3.84	0.5	-8.3	<0.001
Mother's origin (0=wild born)	0.26	0.24	1.09	0.27
Mother's living status (0=dead)	-0.2	0.33	-0.62	0.54
Birth order (0=not first born)	0.21	0.28	0.76	0.45
Age difference: 6-10 years younger	0.15	0.64	0.25	0.8
Age difference: 11-15 years younger	2.4	1.53	1.58	0.11
Age difference: 0-5 years older	-0.27	0.71	-0.38	0.7
Age difference: 6-10 years older	0.03	0.64	0.05	0.96
Age difference: 11-15 years older	-0.29	1.03	-0.29	0.77
Female age*Age difference: 6-10 years younger	0.004	0.1	0.04	0.96
Female age*Age difference: 11-15 years younger	-0.4	0.23	-1.57	0.12
Female age*Age difference: 0-5 years older	0.05	0.12	0.45	0.65
Female age*Age difference: 6-10 years older	-0.08	0.12	-0.65	0.51
Female age*Age difference: 11-15 years older	-0.12	0.22	-0.55	0.58

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538 **Table 5: Time-event model of maternal sister age difference on middle-aged female reproduction (ages 22-**
 539 **43) in Asian elephants.** Terms retained and rejected in the final model (determined using AIC) are shown above
 540 and below the intercept, respectively. Mother's identity was fitted as a random term.

Term	Estimate	Standard Error	Z value	P value
Female age	-0.2	0.02	-1.4	0.16
Age difference:11-15 years older	-6.19	3.5	-1.7	0.07
Female age*Age difference: 11 - 15 years older	0.3	0.18	1.9	0.06
Intercept of Full Model	-2.04	0.54	-3.8	<0.01
Mother's origin (0=wild born)	0.28	0.21	1.32	0.18
Mother's living status (0=dead)	-0.19	0.23	-0.8	0.4
Birth order (0=not first born)	-0.01	0.25	-0.05	0.96
Age difference: 0-5 years younger	-0.63	1.27	-0.49	0.62
Age difference: 6-10 years younger	-1.5	1.17	-1.3	0.18
Age difference: 11-15 years younger	-0.8	1.4	-0.5	0.56
Age difference: 0-5 years older	1.79	1.3	1.3	0.18
Age difference: 6-10 years older	1.3	1.9	0.67	0.5
Female Age*Age difference: 0-5 years younger	0.02	0.04	0.46	0.64
Female age*Age difference: 6-10 years younger	0.05	0.04	1.29	0.19
Female age*Age difference: 11-15 years younger	0.02	0.05	0.5	0.62
Female age*Age difference: 0-5 years older	-0.05	0.05	-1.03	0.3
Female age*Age difference: 6-10 years older	-0.04	0.07	-0.6	0.55

544
 545 **Figure 1: Presence of maternal sister and mean annual probability of female reproduction in Asian**
 546 **elephants.** Sister presence improves female reproduction with an age-specific effect whereby younger females
 547 benefit from the presence of such relatives. Each line grouping represents predictions made by the three Final
 548 Models (Tables 1-3), broken down by age grouping (ages 12-21: N=598; ages 22-43: N=510; ages 44-50:
 549 N=137). Each point represents the mean of the annual probability of reproduction from the raw data. Error bars
 550 represent 95% standard error.

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 552 **Figure 2: Presence of maternal sister (0 to 5 years younger) and mean annual probability of young female**
 553 **reproduction in Asian elephants.** Young females (N=151) living near a sister 0 to 5 years their junior are more
 554 likely to reproduce, compared to young females without a sibling in this age range present. This effect is age-
 555 specific and diminishes over time as females age. Lines represent Final Model predictions (Table 4) and points
 556 represents the mean of the annual probability of reproduction from the raw data. Error bars represent 95%
 557 standard error.
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