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1 ORIGINAL ARTICLE

2 Title: Influence of environmental conditions on population growth and age-specific vital
3 rates of a long-lived primate species in two contrasted habitats

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11 ABSTRACT

As wildlife is increasingly affected by environmental change, identifying how vital 12 rates vary with ecological factors is essential to predict the consequences of environmental 13 perturbations on wild population dynamics. We explored the effects of habitat constraints on 14 the demographic and life history patterns of two Barbary macaque (Macaca sylvanus) 15 populations living in two contrasted habitats in Algeria. Using 11 years of field data, we 16 17 estimated age-specific survival rates of females and of infants of both sexes, as well as female reproduction rates. We investigated how these vital rates were influenced by both intra- and 18 inter-habitat environmental variations. We parameterized age-structured female-only 19 transition matrices and conducted a prospective analysis to estimate the contribution of each 20 vital rate to the populations' asymptotic growth rates (λ). A retrospective analysis (LTRE, 21 Life Table Response Experiment) was also conducted to determine how each vital rate 22 23 contributed to the observed differences in λ between populations. The macaques exhibited 24 common patterns of survival and reproduction (low rates at young ages, and then high and 25 stable until a decrease at old ages), with first evidence of both actuarial and reproductive senescence. Both populations were growing. In both populations, adult and immature survival 26 27 had the highest elasticities, and remained stable in changing environmental conditions. By contrast, infant survival and female reproduction had low elasticities, and varied more with 28 29 environmental variations. As Barbary macaque habitats are increasingly degrading, we

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provide robust estimates of their vital rates with conservation implications, in particular to
 predict population responses to anthropogenic perturbations.

32 KEY WORDS

33 Environmental variation – *Macaca sylvanus* – Matrix population model – Senescence –
34 Survival analysis

35 INTRODUCTION

In the current context of rapid environmental change, it is becoming increasingly 36 important to understand species-specific population dynamics (reproduction, survival, and 37 growth) under different ecological conditions. This can be achieved using population matrix 38 models, arising from the pioneer work of Leslie (1945). This approach was improved on with 39 40 the works of Hamilton (1966), Goodman (1971), Demetrius (1974) and Caswell (1978) who investigated the sensitivity of a population's growth rate to small changes in age-specific vital 41 rates (i.e. birth and death rates), and Tuljapurkar (1980,1989) who included environmental 42 stochasticity in population matrix models. Understanding how environmental variations affect 43 the demographic success of endangered species is particularly critical to inform conservation 44 strategies. Proper management and conservation of endangered species also requires reliable 45 estimates of their demographic parameters (Conde et al., 2019). 46

Mammals share classical patterns of survival and reproduction, with low survival rates 47 48 in juveniles, then high and stable survival rates in adults, followed by a decrease in old adults at the age of actuarial senescence (Caughley, 1966). Reproduction rates are generally low at 49 50 the beginning of sexual maturity and rise to a peak, until they fall at the age of reproductive senescence (Emlen, 1970; Lemaître et al., 2020). When studying population dynamics of 51 52 long-lived species, age is an essential factor to consider, as many variations in environmental 53 conditions affect age-classes differently (Borrego et al., 2008; Coulson et al., 2001; Pardo et 54 al., 2013), and variations in the vital rates of different age-classes affect population growth differently. In long-lived mammals, adult survival is known to often have the highest 55 elasticities, meaning that changes in adult survival tend to have a greater impact on population 56 growth rate than changes in any other vital rate (Gaillard et al., 2000; Heppell et al., 2000). 57 Adult survival also tends to be less affected by environmental variations than reproduction or 58 juvenile survival. For instance, in many ungulate species, decreases in food supply have been 59 shown to reduce female reproductive success and/or juvenile survival, but not adult survival 60 [reindeer (Rangifer tarandus tarandus), Skogland (1985); wild horses (Equus caballus), 61

Dawson & Hone (2012)]. Strong evidence that prey availability affects breeding probability
but not adult survival was also found in carnivores [arctic foxes (*Vulpes lagopus*), Chevallier
et al. (2020); spotted hyenas (*Crocuta crocuta*), Watts & Holekamp (2009)].

Primates are among the mammals with the slowest life histories, and despite great 65 66 diversity and variation among the primate order, their life histories are uniquely slow in comparison to other mammals of the same size (Zimmermann & Radespiel, 2007). They are 67 characterized by long lifespans, slow growth, late ages of first reproduction, and low fertilities 68 compared to most other mammals (Jones, 2011). Survivorship rather than reproduction has 69 70 been shown to consistently have the greatest impact on population growth in diverse primate species and families such as atelids, cercopithecids, cebids, aotids (Alberts & Altmann, 2003; 71 72 Anderson et al., 2019; Blomquist et al., 2009; Hernández-Pacheco et al., 2013; Morcillo et al., 73 2020; Morris et al., 2011), indriids (Dunham et al., 2008; Morris et al., 2011) and hominids 74 (Morris et al., 2011; Robbins et al., 2011). Several studies found that food availability 75 strongly influences female reproduction in primates [Japanese macaque (Macaca fuscata), 76 Takahashi (2002); Assamese macaque (Macaca assamensis), Heesen et al. (2013); rhesus macaque (Macaca mulatta tcheliensis), Cui et al. (2020); chimpanzee (Pan troglodytes), 77 Anderson et al. (2006)] but its effects on age-specific survival remain unexplored. 78

79 The Barbary macaque (Macaca sylvanus) lives in temperate mountainous forests characterized by dry summers and cold winters (Ménard & Vallet, 1996), in Algeria and 80 Morocco. It is an endangered species (Wallis et al., 2020) whose general decline and 81 fragmentation of populations result mainly from forest degradation through overgrazing by 82 domestic herds and inadequate forest management (Ménard et al., 2014a), and the illegal pet 83 trade of infants (Ménard et al., 2014b; van Lavieren, 2008). In addition, climate change is 84 85 expected to induce a dramatic reduction in cedar forests in Algeria and Morocco in the future (Abel-Schaad et al., 2018; Arar et al., 2018; Cheddadi et al., 2009), making it increasingly 86 important to understand how habitat quality affects Barbary macaque demographics. A 87 previous study conducted on different populations living in contrasted forest types showed 88 89 that, whatever the forest, interannual variation of food production with a reduction of staple foods increased infant mortality (Ménard & Vallet, 1993a). In addition, a global analysis 90 91 showed no difference in female reproduction rates between populations while infant mortality 92 tended to be higher in the less suitable forest (Ménard & Vallet, 1993a).

In this study, we explore the demographic and life history patterns of two Barbary macaque populations in two contrasted habitats, and their consequences on population

growth. Using modelling approaches and 11 years of field data on these two populations, we 95 investigate in detail age-specific vital rates, and how they vary depending on environmental 96 conditions. Unlike most similar studies which focus on intra-habitat variations, ours focuses 97 on both intra- and inter-habitat variations. First, we hypothesize that Barbary macaques 98 should exhibit classical long-lived mammal patterns of age-specific vital rates with low infant 99 survival, and high immature and young adult survival followed by a decrease in survival rates 100 in old individuals (i.e. actuarial senescence; Caughley, 1966). Likewise, reproduction rates in 101 young adult females are expected to be low, increase up to mid-age and then decrease 102 103 progressively until death (i.e. reproductive senescence; Lemaître et al., 2020). To test these hypotheses, we estimate female age-specific survival and reproduction rates in each 104 105 population, and compare them between age-classes. Second, we hypothesize that, like in other 106 primates and mammals with slow life histories, female adult survival is the most influential 107 vital rate for population growth in Barbary macaques (i.e. with the highest elasticity) and remains unaffected by variations in food supply, while infant survival and female 108 109 reproduction have the lowest elasticities and vary according to changes in food supply (Heppell et al., 2000; Dawson & Hone, 2012). To test these hypotheses, we compare the age-110 111 specific vital rates of females between populations, as well as between years of normal and bad food production within each population. We also investigate how habitat, inter-annual 112 levels of food production, and seasonal variations affect infant survival rates of both sexes. 113 Finally, we build female-based matrix population models to estimate the asymptotic growth 114 rates of both populations, and investigate the influence of vital rates on asymptotic population 115 growth rates through both prospective and retrospective perturbation analyses. We then 116 discuss the implications of these results for the conservation of Barbary macaques. 117

118 MATERIALS AND METHODS

119 Study species and sites

Barbary macaques live in large polygynandrous multimale-multifemale groups with fairly balanced sex-ratios. Females are strictly philopatric while males are the dispersing sex. Reproduction is highly seasonal, with a mating season in November-December and a birth season in May-July after a 5.5 months gestation period (Ménard & Vallet, 1993a). Females' first conceptions usually start when they reach 5 years of age, but can occur at as early as 4 years of age, and infants are fully weaned at 6 months of age, in September-October (Ménard & Vallet, 1993a).

The two studied groups of Barbary macaques were located in Algeria in a deciduous 127 oak forest (Akfadou, 4°33'E, 36°27'N) and in an evergreen cedar-oak forest (Tigounatine, 128 Djurdjura National Park; 4°8'E, 36°27'N). Previous studies on the ecology and dynamics of 129 those groups have shown that the Tigounatine cedar-oak forest is more favorable for Barbary 130 macaques than the Akfadou oak forest due to a greater specific diversity at all vegetation 131 layers, a more even distribution of food production throughout the year, and a shorter and less 132 critical dry period, particularly for the herbaceous layer, lasting from July to October in 133 Tigounatine vs. June to November/December in Akfadou (Ménard & Vallet, 1988; 1993a). 134

135 Observations were carried out from April 1983 to October 1991 in Akfadou and from April 1983 to July 1993 in Tigounatine to cover the birth season and part of the mating season 136 137 (see Supporting Information 1 for details). The size of the Akfadou group varied from 38 individuals in 1983 to 50 in 1991. The Tigounatine group increased from 46 individuals in 138 139 1983 to 121 in 1993 (in 1989, the initial group divided into three stable groups (Ménard & 140 Vallet, 1993b), which were considered together in our demographic analysis; see details of the composition of groups in Supporting Information 2). Group composition was assessed during 141 each day of observation. All animals were individually recognized based on individual 142 physical characteristics. The age and sex of each individual was determined using 143 morphological and sexual maturity criteria (for details see Supporting Information 2). 144 Because the fate of dispersing males was not always known, those older than 1-year-old were 145 excluded from our analysis. In the present paper, "infant" refers to individuals between 0 and 146 1-year-old; "immature" to sexually immature females (1-3 years-old); and "adult" to sexually 147 mature females (\geq 4 years-old; see Supporting Information 2 for details). For each infant born 148 during the study period, date of birth, sex, and maternal affiliation were recorded, as well as 149 150 the date of death when applicable. Female and male infants, dependent on their mothers, were presumed to have died if they had disappeared. Because females are strictly philopatric, those 151 152 that disappeared during the study period were most likely dead. Our statistic population includes 242 identified individuals (74 in Akfadou, 168 in Tigounatine). 153

154 Survival analysis

Because 100% of the macaques in both the Akfadou and Tigounatine study groups were individually identified, the probability of observing deaths or disappearances was equal to one. The use of count data rather than capture-recapture models thus appeared most appropriate. We estimated age-specific survival rates using the Kaplan-Meier method (Kaplan & Meier, 1958) and tested the effects of population and food production on survival using

Cox proportional hazards models (Therneau & Grambsch, 2000). Those effects were tested 160 161 separately for infants, immatures, and adults. Because the age of females who were older than ten years-old at the beginning of the study (seven individuals) was approximated within a 162 range of 2-3 years (see Supporting Information 2 for details), the adult survival model 163 included a quality factor with two modalities: either known-age or approximated age. Infant 164 survival was estimated on a monthly basis of 1 to 12 months and included both sexes. The 165 effect of sex on infant survival was tested as well. Because there were few females in age-166 classes over 11 years-old, age-classes between 11 and 15 years-old were grouped together, 167 168 and so were age-classes over 16 years-old. This was to avoid over-estimating the survival rates of age-classes which only included one female. The effect of food production was 169 included by categorizing each year as either a "normal" or a "bad" year regarding the 170 availability of two staple foods for the macaques: caterpillars and acorns. Data on these staple 171 172 food abundances are available from 1983 to 1989 (Ménard & Vallet, 1993a). Caterpillars were a valuable source of proteins for macaques the years they invaded oaks in spring. 173 174 However, when they proliferated, the defoliation of oak trees resulted in a low production of acorns the following fall. When caterpillars were unabundant the following year in spring, 175 176 then staple foods were lacking for macaques in two successive critical seasons (*i.e.* during the 177 gestation period and the birth season). Years involving these two successive events were qualified as "bad" years. They occurred in 1986 and 1987 in Akfadou, and in 1984 and 1988 178 in Tigounatine. Normal years were those when at least one of the two staple foods were 179 abundant either in the spring, or in the previous fall. Data from 1990 to 1993 were excluded 180 because of a lack of resource abundance estimation. The effects of population and food 181 production on survival were thus tested in separate models, as they were based on different 182 183 datasets.

We also investigated if infant mortality varied depending on the period of the year. 184 Three periods were considered according to climate and resource availability. The spring 185 period from April to June corresponds to the regrowth of vegetation and the birth season. The 186 dry period includes summer and part of fall (from July to October, hereafter "summer"), 187 which corresponds to a food shortage period due to the desiccation of the herbaceous layer. 188 The third period, when infants are weaned, includes the rest of fall and winter (from 189 November to March, hereafter "winter"), with fall corresponding to an increase in rainfall, 190 with the regrowth of the herbaceous vegetation and acorn production, followed by a wintering 191 food shortage, especially during snowy periods (Ménard & Vallet, 1997). The effect of the 192 193 period on infant survival was tested using Cox proportional hazards models. Individuals that were still alive by the end of the study period were right-censored, as their true survival timewas not known.

196 If models departed from the assumption of proportional hazards, parametric 197 Accelerated Failure Time (AFT) models were constructed. Several classical survival 198 distributions were tested (Weibull, exponential, gaussian, logistic, log-normal and log-199 logistic). Model selection was based on Akaike's information criterion corrected for small 200 sample size (AICc; Burnham & Anderson, 2002) and estimated Akaike weights (R package 201 *"AICcmodavg"*, Mazerolle, 2020). Survival analyses were performed in R statistical package 202 (R Core Team, 2020) with the add-on *"survival"* package (Therneau & Grambsch, 2000).

203 **Reproduction analysis**

Female age-specific reproduction rates were estimated for each population with the nonlinear least squares method using an *ad hoc* adaptation of the fecundity function by Plantegenest et al. (1996), with an increasing function combined with a decreasing exponential to fit the data, such as:

208 (1)
$$y = a\sqrt{(x-x_0)}exp^{-b(x-x_0)}$$

where *y* is the reproduction rate at age *x*; x_0 is the age at first reproduction; *a* is the baseline reproduction rate and *b* is a senescence coefficient.

By derivation of (1), we also observe that the age at maximum reproduction has the simple expression:

213 (2)
$$x_M = x_0 + \frac{1}{2b}$$

214 depending only on the age at first reproduction and the senescence rate. For convergence purposes, x_0 was set to 4 years-old, which is the age at which first conceptions can occur in 215 216 female Barbary macaques (Ménard & Vallet, 1993a). The model was weighted by the number of females in each age-class. The uncertainty of each point estimate was evaluated by 217 218 approximating 95% confidence intervals using an inverse regression ("investR" package in R, Greenwell & Schubert Kabban, 2014). Statistical significance of differences in coefficients a 219 and b between populations was assessed by multivariate Hotelling's T² test and post-hoc two-220 tailed t-tests with non-integer degrees of freedom (Satterthwaite, 1946). 221

222 **Population growth and key parameters**

223 *Model structure*

In order to estimate asymptotic population growth rates and the key parameters influencing those rates, we parameterized two female-only transition matrices (one for each population) according to a birth-pulse post-breeding census design following Caswell (2001), meaning that the censuses occurred immediately after the breeding period, with a 1-year projection interval. Because our study groups had a maximum of 24 ages-classes (from 0 to 23 years-old), the matrices' dimensions were 24x24. The survival rates estimated using the Kaplan-Meier method (Kaplan & Meier, 1958; see section "Survival analysis") and reproductive rates estimated using non-linear regression (see section "Reproduction analysis") were used in the matrices. Because the matrices were female only, reproductive entries in the matrices were multiplied by the sex ratio at birth, calculated as:

234 (3)
$$SR = 1 * N_F / (N_F + N_M)$$

- with N_F being the number of females at birth, and N_M the number of males at birth. Sex ratios at birth were 0.47 in Akfadou and 0.55 in Tigounatine. Reproductive entries in the matrices were:
- 238 (4) $R_i * S_{i-1} * SR$
- with R_i being the reproductive rate at age *i* (*i.e.* the number of infants produced alive per year by a female of age *i*), S_i the female survival rate at age *i*, and *SR* the sex ratio at birth. Survival entries in the matrices were S_i .
- Because age-classes between 11 and 15 years-old, and over 16 years-old were grouped in the 242 survival analysis (see Methods, section "Survival analysis"), survival matrix entries were 243 repeated each year within those stages (see matrix format and values in Supporting 244 Information 3, Tables S3-S5). From the matrices, we estimated the asymptotic population 245 growth rates (λ) as the dominant eigenvalues and investigated variations in λ through 246 prospective and retrospective analyses. The estimated parameters used in the transition 247 248 matrices are given in Table 1 for survival, and Table S6 for reproduction (Supporting Information 3). To compare and test differences in λ between populations, we bootstrapped 249 the original data with replacement 1000 times. We estimated age-specific survival and 250 reproduction rates from the 1000 resulting datasets, and constructed 1000 matrices per 251 population. We then estimated 95% confidence intervals from the resulting 1000 values of λ 252 obtained for each population. 253
- 254 Prospective analysis
- Prospective analyses address the effects that potential future changes in matrix elements may have on λ . Sensitivity (s_{ij}) refers to the change in λ resulting from an absolute change in a matrix element (a_{ij}) and can be calculated from the right eigenvector of the matrix (w) which gives the stable stage distribution, and the left eigenvector (v) which gives the stage-specific reproductive values (Caswell, 2001). It is calculated as:

260 (5)
$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle w, v \rangle}$$

Elasticity is a measure of proportional sensitivity. The elasticity (e_{ij}) of λ to a matrix element (a_{ij}) refers to the proportional change in λ resulting from a proportional change in a_{ij} (Caswell, 2001). It is calculated as:

264 (6)
$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

265 *Retrospective analysis*

Retrospective analyses look back on variations in λ which occurred between two or more sets of environmental conditions, and quantify the contribution of each of the vital rates to the variability in λ (Horvitz et al., 1997). We used a fixed-design Life Table Response Experiment (LTRE) analysis to assess how each vital rate, relative to the others, contributed to variations in λ between the two populations. The difference in λ between both populations, $\Delta\lambda$, is given by (Caswell, 2001):

272 (7)
$$\Delta \lambda = \lambda^{t} - \lambda^{c} \approx \sum_{ij} \left(a_{ij}^{t} - a_{ij}^{c} \right) * \frac{\partial \lambda}{\partial a_{ij}} \left| \frac{A^{t} + A^{c}}{2} \right|$$

Where $(a_{ij}^t - a_{ij}^c)$ is the difference in a_{ij} between the "treatment" matrix (arbitrarily chosen to be Akfadou) and the "control" matrix (arbitrarily chosen to be Tigounatine). $\partial \lambda / \partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} calculated for the mean matrix between the treatment matrix (A^t) and the control matrix (A^c) . For easier readability, the contributions of the different vital rates were summed within stages immatures (1 to 3 years-old) and adults (4 to 15 years old) in both prospective and retrospective analyses. All matrix analyses were performed using the "*popbio*" package in R (Stubben & Milligan, 2007).

280 **RESULTS**

281 Survival

Female age-specific survival rates were estimated from 41 females in Akfadou, and 100 282 females in Tigounatine. During the study period, 22 (54%) females died in Akfadou, and 38 283 (38%) in Tigounatine. Thirteen out of 28 infant females died in their first year in Akfadou, 284 and 16 out of 68 in Tigounatine. Nine out of 31 infant males died in their first year in 285 Akfadou, and 11 out of 51 in Tigounatine. Two infants in Akfadou, and four in Tigounatine 286 died before their sex could be determined. For infants whose death dates were known within a 287 5-months accuracy due to the observation schedule, the retained age of death was the median 288 289 age within the range of possible death ages. The death dates of four females (one in Akfadou and three in Tigounatine) and four males (one in Akfadou and three in Tigounatine) were not 290

known within a 5-months accuracy. Those infants were thus removed from the seasonal infantsurvival analysis, but not from the population and year type analysis.

293 *Survival between populations and year type (years of normal or bad food production)*

294 According to the Cox regression models, infant mortality markedly differed between populations regardless of sex, with infants in Akfadou showing an increased risk of death by 295 210% (39% deaths, N=61 infants) relative to infants in Tigounatine (25% deaths, N=123 296 infants; Hazard ratio = 3.10; 95% CI = 1.41 - 6.79; Table 2). The survival of either immature 297 or adult females did not differ between populations (Table 2). The quality factor accounting 298 299 for the uncertainty of some females' age had no effect on female adult survival (p = 0.43). The survival probability of female infants was 0.74 in Akfadou and 0.82 in Tigounatine 300 301 (Figure 1, Table 1). The survival probability of females was relatively stable for all age classes from one to 15 years-old, with an average of 0.97 in Akfadou 0.98 in Tigounatine. In 302 303 both populations, there was a considerable decrease in female survival after 16 years-old (0.63 in Akfadou and 0.57 in Tigounatine). The oldest age in Akfadou was 17 years-old vs. 23 in 304 305 Tigounatine.

In both populations, infants born in years of bad food production survived less relative 306 307 to infants born in years of normal food production, showing an increased risk of death by 168 % in Akfadou (bad years: 57% deaths, N=21 infants; normal years: 31% deaths, N=32 infant; 308 Hazard ratio = 2.68; 95% CI = 1.16 - 6.23, Table 3) and 593% in Tigounatine (bad years: 309 64% deaths, N=14 infants; normal years: 15% deaths, N=59 infants; Hazard ratio = 6.93; 95% 310 CI = 2.72 - 17.64, Table 3). There was no detectable effect of year type on the survival of 311 immatures and adults (Table 3). However, because no immatures died in Akfadou during bad 312 years, a reliable β coefficient for this category could not be estimated. The effect of year type 313 on immature survival was thus tested only in Tigounatine. 314

315 Seasonal infant survival

When considering seasonal infant survival, data departed from the assumption of 316 proportional hazards ($\chi^2 = 9.5$, p = 0.008). Parametric AFT models were thus compared, and 317 318 models with a log-normal distribution were retained (Table S7 in Supporting Information 3). In both populations, season had a detectable effect on infant survival (Table 4). In Akfadou, 319 320 survival time decreased by 48% and 49% in spring and summer respectively relative to winter (Spring: Time ratio = 0.52, 95% CI = 0.30 – 0.90; Summer: Time ratio = 0.51, 95% CI = 0.30 321 -0.88; Table 4). In Tigounatine, survival time in summer, but not in spring, decreased 322 relative to winter, by 39% (Time ratio = 0.61, 95% CI = 0.40 - 0.92; Table 4). 323

324 **Reproduction**

Reproduction data was obtained from 170 and 476 female-years in Akfadou and 325 Tigounatine, respectively. The mean age at first parturition was 5.25 years-old in Akfadou 326 and 5.61 years-old in Tigounatine, which were not significantly different (W = 195, p = 0.17). 327 In Akfadou, the reproduction rate increased progressively from 0.59 at 5 years-old to 0.84 at 8 328 years-old, its maximum. The onset of reproductive senescence occurred at 9 years-old, when 329 reproduction rates started decreasing progressively until reaching a low of 0.54 at 17 years-330 old (Figure 2, Table S6 in Supporting Information 3). In Tigounatine, the reproduction rate 331 increased progressively from 0.46 at 5 years-old to 0.78 at 10 years-old. The onset of 332 333 reproductive senescence occurred at 13 years-old, and the reproductive rate reached a low of 0.54 at 23 years-old (Figure 2, Table S6 in Supporting Information 3). Age-specific 334 335 reproduction rates did not differ between populations, as shown by the overlapping 95% confidence intervals at all point estimates (Figure 2, Table S6 in Supporting Information 3). 336 Hotelling's T^2 test revealed differences in *a* (baseline reproduction) and *b* (senescence) 337 coefficients between populations ($T^2 = 118.54$, df = 2/39, p <0.001). Post-hoc t-tests failed to 338 339 evidence significant differences in *a* between populations (Akfadou: a = 0.67; Tigounatine: *a* = 0.48; t = 1.90, df = 22.5, p = 0.07), although an effect size corresponding to a variation of 340 341 26% was found (d = 0.55). Coefficient b was higher in Akfadou than Tigounatine (Akfadou: b= 0.13; Tigounatine: b = 0.07; t = 2.25, df = 22.9, p = 0.03), meaning that reproductive 342 senescence was faster in Akfadou. 343

In Akfadou, age-specific reproduction rates did not differ between years of normal and bad food production, as shown by the overlapping 95% confidence intervals at all point estimates (Table S8 in Supporting Information 3). In Tigounatine, reproduction rates of females aged between 8 and 14 years-old were higher in years of normal food production (Table S9 in Supporting Information 3).

349 Asymptotic population growth and key parameters

The asymptotic growth rate in both groups was higher than one, indicating that vital rates were high enough to ensure positive growth in both populations. No detectable differences in λ (Akfadou: $\lambda = 1.08$, 95% CI: 1.05 – 1.10; Tigounatine: $\lambda = 1.10$, 95% CI: 1.09 - 1.12) could be evidenced between populations.

354 *Prospective analysis*

The contribution of the different vital rates to λ were very similar between the two populations (Figure 3), with adult and immature survival accounting for about 51% and 29%, respectively, of the overall elasticity. Infant survival and adult reproduction each accounted for 10%.

359 *Retrospective analysis*

The LTRE analysis showed that all vital rates were lower in Akfadou compared to Tigounatine and contributed to the lower population growth recorded in Akfadou. The survival of infants contributed the most (45%), followed by adult reproduction (40%; Figure 4). Immature and adult survival contributed by 9% and 6%, respectively (Figure 4).

364 **DISCUSSION**

Our analysis of Barbary macaque demography in two contrasted populations revealed that both the cedar-oak forest and the oak forest provided sufficient resources for the groups to yield positive growth. Patterns of elasticities were similar in the two populations and were consistent with other studies showing that, in long-lived species, the survival of adults has the greatest impact on population growth rates (Gaillard et al., 2000; Heppell et al., 2000). Infant survival had a low elasticity, but was the most variable vital rate, which explains why it made such a large contribution to variations in λ between populations.

372 Infant survival was the most variable demographic parameter regardless of sex, decreasing 373 in relation to poor environmental conditions. Inter-population variations were likely due to climatic differences between habitats: the Tigounatine cedar-oak forest, with its higher 374 375 altitude and wetter climate, shows a less critical dry period with a shorter and later period of desiccation of the herbaceous layer. This results in more diverse and abundant resources 376 compared to the Akfadou oak forest, particularly in June (Ménard & Vallet, 1988). These 377 patterns also explain why both spring and summer were critical periods for infant survival in 378 379 Akfadou, vs. only summer in Tigounatine. During the food shortage of the dry period, infants depend entirely on their mothers' milk production, which may not be sufficient to insure their 380 survival. Due to food shortages, cold temperatures and snowy periods in both habitats, winter 381 382 could have been expected to be the most critical period for infant survival. However, infants are weaned in September-October, which coincides with the abundant production of acorns, a 383 384 staple food representing up to 60% of the monthly diet of Barbary macaques in the fall (Ménard & Vallet 1997). Infants are thus able to build up advantageous fat reserves to face 385 386 the following winter. They also benefit from social thermoregulation protecting them from the 387 cold (Campbell et al., 2018), with several individuals (including the mothers and usually their 388 closely related conspecifics) aggregating around the infants and keeping them warm. The high variability of infant survival in relation to environmental variations, compared to other age-389 390 classes in our study, is biologically consistent with the fact that infants, in order to achieve proper growth and physical development, require more energy per unit of body weight than 391

do adults (Ullrey et al., 2003). It was demonstrated in several mammal species, most notably in ungulates, that infant survival is reduced when food supply decreases, while adult survival is unaffected (Dawson & Hone, 2012; Gaillard et al., 1998; Skogland, 1985). In primates, however, there is little information on the effects of food availability on age-specific survival and, to our knowledge, the present study is one of the first to demonstrate the effects of food availability on different age-classes in macaques.

Reproduction rates varied in Tigounatine between normal and bad food production years. 398 This is consistent with other studies finding that variations in food availability affect the 399 400 reproductive success of females in long-lived mammals (Chevallier et al., 2020; Dawson & Hone, 2012; Skogland, 1985; Watts & Holekamp, 2009), including primates (Heesen et al., 401 2013; Takahashi, 2002). The terminal investment hypothesis predicts that an individual's 402 investment in current reproduction should increase when its expectation of future offspring 403 404 decreases through increased mortality risk (Clutton-Brock, 1984). There is a threshold of 405 threat intensity at which individuals are expected to shift their reproductive allocation from 406 favoring survival by reducing current reproduction effort, to the reverse (Duffield et al., 2017). This threshold depends on both intrinsic (e.g. age) and extrinsic (e.g. environmental 407 conditions) factors, and decreases as age increases (Duffield et al., 2017). When 408 environmental conditions decrease to a non-life-threatening level, then prime-aged females 409 should decrease reproductive effort to increase somatic maintenance and delay reproduction 410 until conditions improve. Older females, however, which have a lower survival probability 411 412 due to age, and hence a lower number of potential future breeding attempts, should invest more in reproduction. Our results are in accordance with this theory, as the reproductive rates 413 of females between 8 and 14 years-old in Tigounatine decreased in years of bad food 414 415 production, but not those of females older than 14 years-old.

Age-specific patterns of reproduction followed a classical pattern in both groups [low 416 417 reproduction rate at the beginning of sexual maturity, then reaching a peak at a middle age, and gradually decreasing at oldest ages (Lemaître et al., 2020)]. Although we were not able to 418 419 identify differences in age-specific reproduction rates between populations, our results show that females in Akfadou exhibited a steeper rate of reproductive senescence than females in 420 421 Tigounatine. It is now recognized in the life history theory of aging that variations in 422 environmental conditions influence actuarial senescence (Austad, 1993; Lemaître et al., 423 2013), but little is known of their effects on reproductive senescence. Indeed, most studies focus mainly on the impacts of environmental conditions during development and early life 424

rather than conditions during the entire or late life (Lemaître & Gaillard, 2017). For instance,
in female red deer (*Cervus elaphus*; Nussey et al., 2007) and barn swallows (*Hirundo rustica*;
Balbontín & Møller, 2015), individuals experiencing intense competition during early life
showed faster rates of reproductive senescence in late life. Our results have shown that early
life conditions are more critical for Barbary macaques living in Akfadou than in Tigounatine,
which is coherent with a faster rate of reproductive senescence in adult females from
Akfadou.

Females in our study groups experienced reproductive senescence but not complete 432 433 reproductive cessation, unlike captive female Barbary macaques, who commonly experienced a post-reproductive lifespan of \geq 5 years in Salem, Germany (Kuester et al., 1995; Paul et al., 434 435 1993). Females in Salem ceased reproduction in the second half of their third decade of life, similarly to what was found in captive pig-tailed (Macaca nemestrina) and rhesus (Macaca 436 437 mulatta) macaques (Ha et al., 2000; Walker, 1995). Females in our study did not reach such old ages, the oldest dying around 23 years-old, showing that Barbary macaques with extended 438 439 lifespans in captive conditions can exhibit post-reproductive lifespans, while wild individuals may not. Although several studies suggest that post-reproductive lifespan is a common trait in 440 mammals (Cohen, 2004; Walker & Herndon, 2008), Ellis et al. (2018) showed that it is in fact 441 rare and that the post-reproductive lifespans observed in captive populations are an artifact of 442 the low-risk environments resulting in artificially prolonged life. Out of 52 mammal species 443 tested (including seven primates), they found evidence of actual menopause only in humans 444 (Homo sapiens), killer whales (Orcinus orca), and short-finned pilot whales (Globicephala 445 macrorhynchus). Favorable environmental conditions in captivity, most notably increased 446 food availability, may also protect against reproductive senescence. Lemaître & Gaillard 447 448 (2017) found that although birth rates in captive ring-tailed lemurs (Lemur catta) were consistently higher in semi-captive conditions compared to wild conditions, the magnitude of 449 450 the difference between the two populations reached its maximum at old ages. Similarly, the onset of reproductive senescence in female Barbary macaques in our study happened much 451 452 earlier than in captive females in Salem (9-13 years-old vs. 20 years-old; Kuester et al., 1995). 453 Our results, taken together with studies on captive Barbary macaques, shed new light on the 454 effects that environments with higher risk in the wild compared to captivity may have on reproductive senescence and menopause. 455

456 Actuarial senescence occurred in a similar fashion in both populations, with survival rates 457 decreasing considerably at 16 years old. Both groups exhibited common patterns of survival

for long-lived mammals (Caughley, 1966), with a low survival probability in the first year of 458 459 life, followed by a relatively high and stable survival until a dramatic decrease at the age of senescence. We found the survival of adults and immatures, which are the parameters with the 460 461 highest impacts on population growth rates, to remain stable through all the studied variations in ecological conditions. This is consistent with the fact that for many organisms, the 462 parameters which contribute the most to population growth are the ones showing the less 463 temporal variability (Pfister, 1998). This pattern, called demographic buffering, is likely a 464 result from natural selection which, in fluctuating environments, is expected to maximize the 465 466 long-run growth rate of a population (Hilde et al., 2020). There is thus a strong selection on vital rates with highest sensitivities to remain fairly stable in changing environmental 467 468 conditions, while vital rates with lower sensitivities can be more variable (Hilde et al., 2020). The parameters which contributed the most to variations in λ between our study populations 469 470 (i.e. infant survival and reproduction) were those that had the lowest elasticities, and the effects of those variations on λ were apparently sufficiently small for the groups to display 471 472 comparable asymptotic population growth rates in both populations. Nevertheless, it is important to keep in mind that both study areas provided sufficient resources for the groups to 473 474 yield positive growth. They were both fairly undisturbed, and fluctuations in food production were sustainable for the groups. Although we do not know the past demographic status of the 475 studied populations, we cannot rule out that the observed positive growth partly resulted from 476 a recovering process from a past detrimental event. Indeed, the two study forests suffered 477 from fires during the Algerian war in the years 1960-1962 and showed signs of progressive 478 recovering twenty years later. At the time of data collection, Barbary macaques were 479 classified as vulnerable on the IUCN Red List, but their status changed to endangered since 480 2008 (Wallis et al., 2020). Their decline results mainly from forest degradation due to 481 overgrazing by domestic herds, deforestation and pruning, resulting in increasing loss of 482 suitable habitats (Camperio-Ciani et al., 2005; Mehlman, 1989; Ménard et al., 2014a). 483 Although the current status of the two studied populations is not known, the Djurdjura 484 485 National Park has suffered an increase in anthropogenic development since 2003 and decreases in biodiversity (Hami, 2021), like most habitats in Barbary macaque geographic 486 487 range. The higher the environmental pressures get, the less likely the vital rates with highest impacts on population growth are to remain stable. In the most severe conditions, they will 488 489 decrease, resulting in an increased extinction risk (Eberhardt, 2002). The impacts of increasing environmental pressures can be expected to be all the more detrimental to Barbary 490 491 macaque demography given that the remaining natural populations are highly fragmented and

experiencing disrupted gene flows and high genetic differentiation (Le Gouar et al., 2021). It 492 is thus becoming increasingly important to implement conservation programs for Barbary 493 macaques, which require a good understanding of how their environment influences their 494 population dynamics. Our 11-year study brought to light new important information on such 495 dynamics, but we do point out that it lasted only half as long as Barbary macaque lifespan. 496 Thus, it does not constitute a full demographic analysis as it did not allow the monitoring of 497 all individuals from birth to death. However, in the absence of longer demographic 498 monitoring of this species, our study brings valuable new insight on its dynamics in relatively 499 500 undisturbed populations in two different habitats with environmental variations. It provides demographic parameters which can be used as useful indicators of population viability in 501 502 conservation programs.

503 Conclusions

This longitudinal study, based on an 11-year-long dataset of two social groups in two 504 505 contrasted habitats, provided essential data on their demographic evolution and life-history traits. The analysis of these data through time-tested mathematical modelling techniques 506 brings us to new, well-founded conclusions. The groups' dynamics depend on habitat type 507 and resource availability. Although the group living in the more favorable cedar-oak forest 508 displays better infant survival, and longer lives, the group living in the oak forest shows no 509 510 sign of critical viability during the study period. When environmental conditions, more specifically food availability, decline, both groups show fairly similar dynamics which are 511 consistent with classical patterns for long-lived vertebrates. Infants are the most impacted 512 513 stage. They exhibit significant decreases in survival probability, while immature and adult survival remain stable. Our study presents important interests for the conservation of the 514 515 endangered Barbary macaque by increasing knowledge on its population dynamics and by providing reliable estimates of its vital rates in wild and relatively undisturbed populations. 516

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536 **Ethics statement**

Our observational study complied with the ethical guidelines of the CNRS/University of
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- 539Park and the Ministère de l'Hydraulique, de l'Environnement et des forêts of Algeria.
- 540 **Conflict of interest**

541 The authors declare no conflict of interest.

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Table 1. Age-specific estimates of survival probabilities of female Barbary macaques in
Akfadou and Tigounatine. Age-classes between 11 and 15 years-old were grouped together,
and so were age-classes over 16 years-old, to avoid over-estimating the survival probabilities
of age-classes which comprised only one female. N = sample size.

		Akfadou		Tigounatine		
	Age	Survival	Ν	Survival	Ν	
Stage	(years)	probability		probability		
Infants	0	0.74	41	0.82	100	
Immatures	1	0.95	25	0.96	74	
	2	0.97	25	0.98	61	
	3	0.97	22	0.97	53	
Adults	4	0.98	21	0.98	45	
	5	0.99	21	0.99	36	
	6	0.99	16	0.99	35	
	7	0.98	12	0.99	31	
	8	0.98	12	0.99	27	
	9	0.96	10	0.96	22	
	10	0.98	9	0.98	21	
	11 to				61	
	15	0.93	25	0.93		
	>16	0.63	4	0.57	23	

Table 2. Results of Cox regression models for the influence of population and sex on infant survival, and of habitat only on immature and adult survival. Immatures and adults included only females. Infants included both females and males. The dataset included years 1983 to 1991 in Akfadou, and 1983 to 1993 in Tigounatine.

	Predictor	β ^a	Hazard ratio ^b	95% CI ^c	p-value
Infants	Population ^d	1.13	3.10	1.41 – 6.79	0.005**
	Sex ^e	-0.22	0.81	0.34 - 1.88	0.618
	Population ^d \times Sex ^e	-0.48	0.62	0.18 - 2.12	0.442
Immatures	Population ^d	-0.31	0.73	0.16 - 3.40	0.692
Adults	Population ^d	0.58	1.78	0.67 – 4.74	0.248

812 ** p-value < 0.005.

813 ^a The sign of the β coefficient indicates either a higher (>0) or lower (<0) risk of death relative

to the reference category.

^b The hazard ratio represents the relative difference between the two categories.

^c 95% Confidence interval (CI) for the hazard ratio.

817 ^d Reference is Tigounatine.

818 ^e Reference is female.

819

821 Table 3. Results of Cox regression models for the influence of year type (normal or bad food 822 production) on infant, immature, and adult survival. Models were separate for each population 823 in each stage. Immatures and adults included only females. Infants included both females and 824 males. The dataset included years from 1983 to 1989 in both populations.

	Predictor	β ^a	Hazard ratio ^b	95% CI ^c	p-value
Infants	Year type ^d				
	Akfadou	0.99	2.68	1.16 - 6.23	0.02*
	Tigounatine	1.94	6.93	2.72 - 17.64	4.9×10 ⁻⁵ **
Immatures	Year type ^d				
	Akfadou	Non-estimable			
	Tigounatine	1.30	3.67	0.67 - 20.07	0.13
Adults	Year type ^d				
	Akfadou	0.55	1.74	0.26 - 11.75	0.57
	Tigounatine	-0.07	0.93	0.09 - 9.01	0.95

825 * p-value < 0.05; ** p-value < 0.005.

^a The sign of the β coefficient indicates either a lower (>0) or higher (<0) probability of

827 survival relative to the reference category.

^b The hazard ratio represents the relative difference between the two categories.

829 ^c 95% Confidence interval (CI) for the hazard ratio.

830 ^d Reference is normal.

Predictor	β ^a	Time ratio ^b	95% CI ^c	p-value	
Season ^d					
Akfadou					
Spring	-0.65	0.52	0.30 - 0.90	0.02*	
Summer	-0.67	0.51	0.30 - 0.88	0.01*	
Tigounatine					
Spring	-0.39	0.68	0.41 - 1.10	0.12	
Summer	-0.50	0.61	0.40 - 0.92	0.02*	

Table 4. Results of Accelerated Failure Time models for the influence of season on infant 831 survival within each population. Both females and males are included.

* p-value < 0.05. 833

832

^a The sign of the β coefficient indicates either an increase (>0) or decrease (<0) in survival 834

time relative to the reference category. 835

^b The time ratio represents the relative difference between the two categories. 836

^c 95% Confidence interval (CI) for the time ratio. 837

^d Reference is winter. 838

839 Legends of figures

Figure 1. Kaplan-Meier survival curves at each habitat. Solid line: Akfadou; dashed line:
Tigounatine; +: censored individuals.

- Figure 2. Observed female reproductive data and estimated reproduction rates in Akfadou
 (solid wide line) and Tigounatine (dashed wide line). 95% confidence intervals are showed
 for Akfadou (solid thin lines) and Tigounatine (dashed thin lines).
- Figure 3. Elasticity of vital rates for Akfadou and Tigounatine. Sin: infant survival; Sim:
 immature survival; Sa: adult survival; Ra: adult reproduction.
- Figure 4. Relative contributions of vital rates to variations in λ in Akfadou compared to Tigounatine. Sin: infant survival; Sim: immature survival; Sa: adult survival; Ra: adult reproduction.







Figure 2







