Family matters: Linking population growth, kin interactions, and African elephant social groups

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Abstract

In many species, individuals are embedded in a network of kin with whom they interact. The interactions among kin may affect the survival and fertility rates, and thus the life history of individuals. These interactions indirectly influence both the network of kin and the dynamics of the population. In this way, non-linear feedback emerges between the kin network and individual life history rates. We describe a model that calculates the kin network of an individual while incorporating the feedback between the network and the life history of the individual. We demonstrate the use of this model for African elephant populations. We incorporate effects of the mother's presence and matriarch age on the survival of juveniles, and of the presence of a sister on the fecundity of young females. We find that interactions between family members amplify the negative effects of poaching on the family structure and growth rate of African elephant populations. Our analysis provides a framework that can be applied to a broad range of of social species.

Introduction

From birth to death, nearly all organisms are embedded in a network of kin. This kinship network typically includes parents and grandparents at the birth of an individual and shifts towards children and grandchildren once an individual starts to reproduce. The kinship network extends beyond the direct parental line of an individual to other related individuals such as sisters, aunts and nieces. The dynamics of the kinship network is closely linked to the life history of individuals and depends on the survival and fertility rates of the individuals within the kinship network (e.g., Caswell, 2019; Caswell and Song, 2021; Coste et al., 2021; Goodman et al., 1974; Jiang et al., 2023).

While all organisms are part of a kinship network, the behavioural and ecological interactions among the members of a kinship network are most important in species with strong social structure (Waldman, 1988). A wide range of plant and animal species exhibit interactions between kin and many of them have the ability to distinguish kin from other individuals. Several evolutionary and ecological mechanisms for the recognition of kin have been proposed and organisms have been shown to utilise a wide range of chemical, olfactory, visual and auditory clues to recognize kin (Penn and Frommen, 2010; Tang-Martinez, 2001). Even if individuals are not able to actively recognise kin, regular interactions between kin may occur due to the co-occurrence of kin in space and time. It is debatable whether interactions between kin that merely emerge from co-occurrence patterns should be linked to the kin network of an individual or to other spatial and temporal patterns and dynamics of the population (Tang-Martinez, 2001).

Some species actively avoid the co-occurrence of closely related kin to minimize negative effects of kin such as inbreeding and kin competition (Bengtsson, 1978; Gandon, 1999; Hamilton and May, 1977; Hohenlohe et al., 2021). This avoidance behaviour can result in interesting dispersal patterns, such as sex-specific dispersal distances and behaviour (Li and Kokko, 2019). Conversely, kin of many species cluster together to benefit from positive interactions between family members like cooperation, alloparenting, knowledge sharing and other forms of assis-

tance (Kramer and Meunier, 2019).

Interactions among kin affect the survival and fertility of individuals and consequently the life history of these individuals. Simultaneously, the kinship network of an individual is shaped by the life history rates in the population (Caswell, 2019). This gives rise to interactive feedback mechanisms between the kinship network and the life history of an individual. Not only do these mechanisms influence individual life histories but they also propagate to the relatedness and dynamics of the entire population, because the dynamics of the population emerge from the integration of the life histories of all individuals in the population (Caswell, 2001).

Feedback mechanisms between the life history and the kinship network of an individual can impact the conservation and protection of species living in family groups. Understanding human and environmental influences on the viability and genetic diversity of a population is crucial for the conservation of a population. The viability of a population is typically assessed by linking individual life history rates to the dynamics of the population through age- or stage-structured models (Akçakaya, 2000; Caswell, 2001). Sometimes these models account for feedback mechanisms between the population and the individual life history rates in the form of defnsity dependence or Allee effects. However, interactions between individual life histories and other levels of organisation such as a family group or the kinship network are usually not accounted for. Anthropogenic influences might strongly affect the composition of family groups or the kin network, consequently altering individual life history rates and the dynamics of the population.

A comprehensive understanding of the genetic diversity and relatedness among individuals is essential to prevent inbreeding and genetic artifacts in a population (Allendorf et al., 2010; Amos and Balmford, 2001; Gobush et al., 2008). Modern techniques using genetic markers offer insight into the current genetic diversity and relatedness of a population. Although these methods could provide an accurate insight in the current genetic diversity of the population, these methods do not predict how the relatedness between individuals in the population will shift due to human and environmental change. The dynamics of the population and the dynamics of the kinship

network are strongly linked to changes in relatedness between individuals in the population and are therefore essential to consider when exploring changes in the relatedness between individuals of a population.

In this paper, we present a model that incorporates feedback mechanisms between the kinship network and the life history rates of an individual. This model connects the dynamics of the kinship network to the dynamics and viability of the population. Our model is based on a matrix approach to the formal demography of kinship, which has been extensively developed for human populations (Caswell, 2019, 2020, 2022; Caswell and Song, 2021; Caswell et al., 2023), but the incorporation of kin interactions remains an open problem.

We illustrate the model by exploring how interactions within family groups of African elephants shape the impact of poaching on the viability and relatedness of an elephant population. Female African elephants live in family groups consisting of related kin and are led by a matriarch which is typically the oldest female in the family group (Athira and Vidya, 2021; Vidya and Sukumar, 2005). The structure of the family groups allows for numerous social interactions between kin, several of which are well quantified in field studies. Meanwhile, adult females are targeted for ivory poaching, which disturbs the structure of these family groups (Archie and Chiyo, 2012). As such, poaching has both direct and indirect effects on the viability of the elephant population, emerging from additional mortality as well as interactions between the family network and individual life history rates. We explore how these interactions shape the response of the population to changes in poaching pressure. To do so, we calculate the population growth rate and expected relatedness of an individual to the members in the kin network, while considering interactions among members of the kin network.

Modelling framework

Notation and terminology

We formulate our model in terms of matrices. Matrices are denoted by uppercase bold characters (e.g., $\mathbf{U}$) and vectors by lowercase bold characters (e.g., $\mathbf{x}$). Vectors are column vectors by default; The transpose of $\mathbf{x}$ is denoted as $\mathbf{x}^{\mathsf{T}}$. The vector $\mathbf{1}$ is a vector of ones. Subscripts are used to refer to a specific entry of a vector; for example, $\mathbf{x}_i$ is the ith entry of vector $\mathbf{x}$. The symbol $\circ$ denotes the Hadamard, or element-by-element product (implemented by .* in MATLAB and by * in R). The function $\mathrm{diag}(\mathbf{x})$ results in a square matrix with the entries of the vector $\mathbf{x}$ on the diagonal. The notation $\|\mathbf{x}\|$ denotes the 1-norm of $\mathbf{x}$. Occasionally, MATLAB notation will be used to refer to rows and columns; for example, $\mathbf{F}(i,:)$ and $\mathbf{F}(:,j)$ refer to the ith row and jth column of the matrix $\mathbf{F}$, respectively.

General framework

Our model framework links the interactions between individual life history rates and the structure of a kin network to the dynamics of the population (Fig. 1). The age-specific survival rates are described in the square survival matrix $\mathbf{U}$ with non-zero survival probabilities on the sub-diagonal and zeros elsewhere. The age-specific reproduction rates are described by the square fertility matrix $\mathbf{F}$ with fertility values in the first row and zeros elsewhere (Caswell, 2001). The size of these matrices corresponds to the number of age classes ω in the model. The survival and fertility matrices project the composition of an extended family network from the perspective of a focal individual. We will refer to the focal individual as Focal (Caswell, 2019). This kinship network describes the age structure of specific types of kin, such as daughters, sisters, nieces, aunts, mothers and grandmothers of Focal at a given age of Focal.

Interactions between family members, such as alloparenting or food sharing, are incorporated into the model by making the entries in the survival and fertility matrices dependent on the

abundance and/or age structure of specific types of kin. This results in feedback between the individual life history rates and the kinship network. The feedback between the individual life history rates and the kinship network translates to a large set of non-linear equations. We use an iterative approach to solve this set of non-linear equations to obtain explicit numerical expression of the age-specific kinship network (supplementary materials). The resulting age-specific kinship network is the kinship network that all individuals are expected to have, considering the included interactions between the kinship network and the life history rates of individuals.

Once the age-specific kinship network is solved, the dynamics of the entire population is modelled by combining the survival matrix $\mathbf{U}$ and fertility matrix $\mathbf{F}$ into a population projection matrix $\mathbf{A}$:

$$\mathbf{A} = \mathbf{U} + \mathbf{F} \tag{1}$$

The long-term population growth rate implied by $\mathbf{A}$ is given by the dominant eigenvalue (λ) of this matrix and is used as a measure of the viability of the population. If $\lambda > 1$ the population will grow. If $\lambda < 1$ the population will decline to eventual extinction. The eigenvector corresponding to the dominant eigenvalue, normalized to sum to one ($\mathbf{w}$), gives the stable age distribution of the population.

In this study we use this framework to explore how poaching impacts the growth rate of an elephant population while considering the feedback between family members and the life history of individuals. We consider scenarios in which the presence of a mother influences the juvenile survival, the presence of sisters increases the fertility of young females and matriarch age increases juvenile survival. For each scenario, we solve the age-specific kinship network and calculate the population growth rate under varying poaching conditions, ranging from no poaching ($\mu = 0$) to high poaching ($\mu = 0.2$). Additionally, we calculate the expected relatedness between an individual and their kin network, to gain insight in the effect of poaching on the kin network of an individual.

In the following sections we will first briefly outline the kinship model developed by Caswell (2019). In addition, we derive some properties of the kinship network that are needed to include

the feedback between the network and the individual life history, for our specific example of African elephants. In the section thereafter we will describe in more detail how these interactions are quantified and included in the survival and fertility matrices of African elephants.

Kinship model

Family groups of African elephants mainly consist of related females and their offspring. Male elephants typically leave the family group during adolescence. We therefore focus on modelling the female part of the kinship network. The kinship network is modelled with an adapted version of the model described by Caswell (2019). Because we assume that the age-specific kinship networks of all individuals are, at a specified age, the same, we need only calculate the age-specific kinship network of one individual, which we refer to as Focal. We indicate the age of Focal with x. Because all individuals have the same age-specific kinship network, the fertility and survival matrices are equal for all individuals in the population as well. Table 1 provides an overview of all kin included in this model.

We will derive age-specific expressions for the probability that an individual has a living mother ($\delta(x)$), the probability that an individual has at least one sister ($\nu(x)$) and the expected oldest age in the family ($\gamma(x)$). These quantities are used to incorporate the interactions between family members in the fertility and survival matrices of African elephants. We use the vector $\mathbf{k}(x)$ to indicate the age structure of kin in equations that apply to all kin. Additionally, we use the vector $\mathbf{z}(x)$ to denote the age structure of all kin combined. Lastly, the vector $\boldsymbol{\phi}(x)$ represents the age structure of Focal, which consists of a one in the row corresponding to the age of Focal (x) and zeros elsewhere.

The dynamics of the age structure of kin is described by a general equation:

$$\mathbf{k}(x+1) = \mathbf{U}\mathbf{k}(x) + \boldsymbol{\beta}(x) \tag{2}$$

In which $\mathbf{U}$ is the survival matrix and $\boldsymbol{\beta}(x)$ is a subsidy term describing the birth of kin from another kin type. To model the dynamics of a kin type, we also need the initial age structure of

this kin type at the birth of Focal ($\mathbf{k}(0)$) (Table 1).

Daughters, granddaughters and great-granddaughters

Daughters ($\mathbf{a}(x)$), granddaughters ($\mathbf{b}(x)$) and great-granddaughters ($\mathbf{c}(x)$) of Focal are only born after Focal. The initial distribution of these kin types at the birth of Focal is therefore always zero ($\mathbf{k}(0) = 0$). The subsidy term of these kin types consists of the distribution of the parent kin multiplied by the fertility matrix. For example, in the case of Focal's daughters, the subsidy term consists of the age distribution of Focal multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\boldsymbol{\phi}(x)$). Similarly, the subsidy term for Focal's granddaughters is the distribution of daughters multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{a}(x)$) and the subsidy term for Focal's great-granddaughters is the distribution of granddaughters multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{b}(x)$) (Table 1).

Mothers, grandmothers and great-grandmothers

The expected age structure of mothers ($\mathbf{d}(x)$) at the birth of Focal ($\boldsymbol{\pi}$) is the age distribution of mothers at the birth of children. It is calculated by weighting the stable age structure of the population ($\mathbf{w}$) by the age-specific fertility and normalizing the resulting vector to sum to one.

$$\boldsymbol{\pi} = \frac{\mathbf{F}(1,:)^{\intercal} \circ \mathbf{w}}{\|\mathbf{F}(1,:)^{\intercal} \circ \mathbf{w}\|} \tag{3}$$

As Focal does not acquire additional mothers during its life, the subsidy term of Focal's mother is zero ($\boldsymbol{\beta}(x) = 0$). The distribution of mothers throughout Focal's life is calculated using only the survival matrix (Table 1). Later we will need the probability that the mother of an individual is alive. Because the number of mothers follows a Bernoulli distribution, the probability of the mother of Focal being alive ($\delta(x)$) is equal to the expected number of mothers. The expected number of mothers at a given age of Focal is calculated by summing the age distribution of mothers of Focal at age x:

$$\delta(x) = \|\mathbf{d}(x)\| \tag{4}$$

Focal's grandmother ($\mathbf{g}(x)$) is the mother of Focal's mother. Assuming equal age-specific family distributions for all individuals, the initial distribution of Focal's grandmother is calculated by weighting the distribution of the mother at age x by the initial distribution of mothers at the birth of Focal ($\mathbf{g}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{d}(i)$).

Similarly, the great-grandmother ($\mathbf{h}(x)$) of Focal is the grandmother of Focal's mother. The initial distribution of great-grandmothers is therefore calculated by weighting the distribution of grandmothers at age x with the initial distribution of mothers ($\mathbf{h}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{g}(i)$). Focal does not acquire new grandmothers or great-grandmothers throughout its life and the subsidy term of these kin is therefore zero ($\boldsymbol{\beta}(x) = 0$) (Table 1).

Sisters

Sisters older than Focal ($\mathbf{m}(x)$) are the daughters of Focal's mother born before Focal's birth. The initial distribution of older sisters is therefore calculated as the distribution of daughters weighted by the distribution of mothers at Focal's birth ($\mathbf{m}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{a}(i)$). After Focal's birth, no new older sisters are born, resulting in a subsidy term of zero for older sisters ($\boldsymbol{\beta}(x) = 0$).

Younger sisters ($\mathbf{n}(x)$) are born after Focal's birth and the initial distribution of younger sisters is therefore zero ($\mathbf{n}(0) = 0$). Younger sisters are the offspring of Focal's mother born after Focal and the subsidy term for younger sisters is therefore the age distribution of mothers multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{d}(x)$).

The offspring of Focal's mother born in the first time step ($x = 0$) include Focal but might also include sisters of Focal if Focal's mother gives birth to multiple offspring at the same time.[1] The expected clutch size ($E(L)$) with Focal is the expected number of offspring conditioned on the birth of Focal ($E(L|L \geq 1)$). This is calculated by correcting the expected clutch size for the probability a clutch is born ($P(L > 0)$). We assume that the number of offspring follows a Poisson

[1] This possibility is explicitly neglected in the development of the matrix kinship model for humans (Caswell, 2019), but may be important for non-human species.

distribution:

$$
\begin{aligned}
E(L|L \geq 1) &= \frac{E(L)}{P(L > 0)} \\
&= \frac{E(L)}{1 - \exp\left(-E(L)\right)} \\
&= \frac{\|\mathbf{F}\boldsymbol{\pi}\|}{1 - \exp\left(-\|\mathbf{F}\boldsymbol{\pi}\|\right)}
\end{aligned}
\tag{5}
$$

The number of sisters born simultaneously with Focal is the expected clutch size conditioned on the birth of Focal minus one. These sisters are, on average, equally divided between older and younger sisters (Table 1).

Later we will need the probability that an individual has at least one sister. The total number of sisters ($v(x)$), is the sum of the younger and older sisters. If we again assume that the number of sisters is Poisson distributed, we can derive the probability that Focal has at least one sister.

$$
\begin{aligned}
\nu(x) &= P(v(x) \geq 1) \\
&= P(v(x) > 0) \\
&= 1 - \exp\left(-E(v(x))\right) \\
&= 1 - \exp\left(-\|\mathbf{m}(x) + \mathbf{n}(x)\|\right)
\end{aligned}
\tag{6}
$$

Nieces, aunts and cousins

The nieces of Focal are the offspring of Focal's older and younger sisters ($\mathbf{p}(x)$ and $\mathbf{q}(x)$ respectively). Focal's older sisters could produce offspring before Focal's birth. The nieces at Focal's birth are the granddaughters of Focal's mother at the birth of Focal. We calculate the initial distribution of nieces through older sisters by weighting the distribution of granddaughters with the distribution of mothers at the birth of Focal ($\mathbf{p}(0) = \sum_i \pi_i \mathbf{b}(i)$). Older sisters might still produce offspring after Focal's birth and the subsidy term of these nieces is therefore the distribution of older sisters multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{m}(x)$).

Younger sisters are not yet born at the time of Focal's birth, so the initial distribution of nieces through younger sisters is zero ($\mathbf{p}(0) = 0$). The subsidy term of nieces through younger sisters is the distribution of younger sisters multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{n}(x)$) (Table 1).

The aunts of Focal are divided into aunts older than Focal's mother ($\mathbf{r}(x)$) and aunts younger than Focal's mother ($\mathbf{s}(x)$). Aunts older than Focal's mother are the older sisters of Focal's mother. We calculate the initial distribution of these aunts by weighting the distribution of older sisters with the distribution of mothers at the birth of Focal ($\mathbf{r}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{m}(i)$). Aunts older than Focal's mother cannot be born after Focal's birth, so the subsidy term for these aunts is zero ($\boldsymbol{\beta}(x) = 0$). Aunts younger than Focal's mother are the younger sisters of Focal's mother. The initial distribution of these aunts is therefore calculated by weighting the distribution of younger sisters with the distribution of mothers at the birth of Focal ($\mathbf{s}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{n}(i)$). Aunts younger than Focal's mother can still be born after Focal's birth. The subsidy term of these aunts is therefore the distribution of grandmothers multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{g}(x)$) (Table 1).

Lastly, both the aunts older than Focal's mother and aunts younger than Focal's mother produce cousins of Focal ($\mathbf{t}(x)$ and $\mathbf{v}(x)$ respectively). The cousins of Focal are the nieces from Focal's mother. The initial distribution of these cousins is calculated by weighting the distribution of nieces with the distribution of mothers at the birth of Focal ($\mathbf{t}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{p}(i)$ and $\mathbf{v}(0) = \sum_i \boldsymbol{\pi}_i \mathbf{q}(i)$). The subsidy terms for cousins are the distribution of aunts older than Focal's mother multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{r}(x)$) and the distribution of aunts younger than Focal's mother multiplied by the fertility matrix ($\boldsymbol{\beta}(x) = \mathbf{F}\mathbf{s}(x)$) (Table 1).

Oldest age in the family

Some of the interactions between family members and individual life history rates depend on the age of the oldest female in the kinship network. The oldest female in the network could be from various types of kin. Let the age distribution of the entire family at age x of Focal be represented by a vector $\mathbf{z}(x)$, calculated by summing the age distributions over all types of kin. Given the age distribution of kin, we derive the expected age of the oldest individual ($\bar{\gamma}(x)$) in the family using order statistics (Wilks, 1948).

The probability that the oldest age in the family is equal to a specific age y is calculated as:

$$P\left(\gamma(x) = y\right) = P\left(\gamma(x) \leq y\right) - P\left(\gamma(x) \leq y - 1\right), \tag{7}$$

in which $P(\gamma(x) \leq y)$ is the probability that the oldest age in the family is equal or below y, which is the same as the probability that all individuals in the family have age y or younger. Similarly, $P(\gamma(x) \leq y - 1)$ is the probability that the oldest age in the family is equal or below $y - 1$, which is the same as the probability that all individuals in the family have age $y - 1$ or younger.

Because we conditioned the model on the survival of Focal, we know that the oldest age in the family is at least as old as the age of Focal (i.e., $\gamma(x) \geq x$). We therefore only include ages equal or older than Focal's age in the following analysis. We can express the probability that the oldest age is equal to y as:

$$P(\gamma(x) = y \mid x) = \left[\frac{\sum_{i=x}^{y} z_i(x)}{\sum_{i=x}^{\omega} z_i(x)}\right]^{\sum_{i=x}^{\omega} z_i(x)} - \left[\frac{\sum_{i=x}^{y-1} z_i(x)}{\sum_{i=x}^{\omega} z_i(x)}\right]^{\sum_{i=x}^{\omega} z_i(x)} \tag{8}$$

The term between the first square brackets is the probability that a family member with an age equal or older than Focal is of age y or younger, calculated as the number of individuals with an age between x and y ($\sum_{i=x}^{y} \mathbf{z}_i(x)$) divided by the total number of individuals in the kin network of the same age as Focal or older ($\sum_{i=x}^{\omega} \mathbf{z}_i(x)$). The term between the second square brackets is constructed in a similar way to calculate the probability that a family member with the same age or older than Focal has age $y - 1$ or younger. These probabilities are raised to the total number of kin with the same age or older than Focal ($\sum_{i=x}^{\omega} \mathbf{z}_i(x)$), to calculate the probability that all kin with the same age or older than Focal are of age y or younger and age $y - 1$ or younger respectively.

It is important to note that these calculations are only relevant for ages above Focal's age ($y > x$) as individuals younger than Focal cannot be the oldest individual in the family ($P(\gamma(x) = y \mid y < x) = 0$). From the probability distribution of the oldest age in the family we can calculate

the expected oldest age in the family, given a specific age of Focal:

$$\bar{\gamma}(x) = E(\gamma(x)|x) = \sum_{y=x}^{\omega} yP(\gamma = y(x) \mid x) \tag{9}$$

Relatedness

Kin types vary in their relatedness to Focal. The kinship model provides the distributions and total count of every kin type at every age of Focal, so we can characterize the kinship network in terms of relatedness.

For instance, Focal's sisters and mother are more closely related to Focal than are Focal's great-grandmothers or cousins. The kinship model is based on female relatedness, so it is evident that all sisters in the kinship model share the same mother. In contrast, the model is ambiguous about paternity. This affects the expected relatedness between kin. If two sisters share the same father, their expected relatedness is 0.5 because the sisters overlap in both the maternally and paternally inherited genes. In contrast, if sisters have different and unrelated fathers, the expected relatedness between the sisters drops to 0.25, because they share only maternal genes. For the relatedness to more distant related kin, we assume that fathers are always unrelated. For example, Focal's sister and Focal might share the same father, but Focal's nieces are assumed to have a father unrelated to the father of Focal. This results in a minimum and a maximum expected relatedness (ζ^k) between Focal and the kin in the kinship network (Table 2).

The age-specific average relatedness of Focal to the members of the family network ($\eta(x)$) is calculated by weighting the relatedness of a kin type by the relative abundance of the kin type in the family.

$$\eta(x) = \sum_k \frac{\|\mathbf{k}(x)\|}{\|\mathbf{z}(x)\|} \zeta^k, \tag{10}$$

in which $\mathbf{k}(x)$ represents the age distribution of kin of type $\mathbf{k}$ at age x of Focal and ζ^k is the relatedness of that kin of type $\mathbf{k}$ to Focal. The expected relatedness of a random individual from the population to its kinship network (ξ) is calculated by multiplying the calculated age-specific average relatedness ($\eta(x)$) with the weighted stable age structure of the population ($\mathbf{w}$) to obtain

the total expected relatedness of a random individual to the members of their family group:

$$\xi = \sum_{i=1}^{\omega} w_i \, \eta(i) \tag{11}$$

Survival and fertility of African elephants

In this study we parameterise the survival and fertility matrices using age-specific estimates for survival and fertility of female African elephants. We include 63 age classes in our model ($\omega = 63$). Survival and fertility values for individuals up to 50 years old are taken from estimates under low poaching conditions by Wittemyer et al. (2021). These estimates are complemented with survival and fertility estimates for females between 51 and 63 years old from the same African elephant population recorded by Wittemyer et al. (2013).

The survival and fertility estimates are smoothed using a Gaussian-weighted moving average with a window of 25 years. After smoothing, the fertility of individuals below 8 years old is set to zero, because females of the African elephant do not mature and reproduce before this age. The resulting survival and fertility matrices are used as a baseline scenario. We assume that, in this baseline scenario, the impact of poaching is minimal (Supplementary figure S1).

Poaching

Poaching is included in the model as a proportional decrease in age-specific survival. (This corresponds to additive mortality hazard, appropriate for risks like harvesting.) To scale poaching mortality, we introduce a parameter μ to vary poaching pressure from zero, indicating no poaching, to one, indicating that all individuals in targeted age classes are killed by poaching. In addition, we introduce a vector $\boldsymbol{\rho}$ of size ω describing the relative age-specific vulnerability to poaching ranging between 0 and 1. Poaching pressure for juveniles below 8 years old is much lower than poaching pressure of older females. The poaching vulnerability of females below 8 years old is therefore set to zero ($\boldsymbol{\rho}(1:8) = 0$). Similarly, adolescents between 9 and 18 years old are approximately half as likely to die from poaching than older females (Wittemyer et al.,

2013). The poaching vulnerability of females between 9 and 18 years old is therefore set to 0.5 ($\boldsymbol{\rho}(9:18) = 0.5$). The poaching vulnerability for females above 18 years old is set to one ($\boldsymbol{\rho}(19:63) = 1$). The survival matrix including poaching ($\mathbf{U}^{\mu}$) is given by

$$\mathbf{U}^{\mu} = \mathbf{U}\ \mathrm{diag}(1 - \mu\boldsymbol{\rho}_i) \tag{12}$$

We will indicate a specific poaching pressure by adding a superscript to matrices and vectors (e.g. $\mathbf{U}^{\mu}$, $\mathbf{k}^{\mu}$).

Family feedback

In the specific case of elephants, the effect of three different interactions within a family group on the survival and fertility rates have been quantified. These interactions are incorporated in our model by making the entries in the survival and fertility matrices dependent on specific characteristics of the kinship network. As we assume that all individuals are identical in their age-specific kinship network, the kin-dependent survival and fertility matrices are the same for all individuals in the family and population. Consequently, we only need to quantify the family structure of a single individual to obtain a survival and fertility matrix applicable to all individuals.

The first quantified effect of family on the life history of elephants is a decrease in juvenile survival in the absence of their mother (Parker et al., 2021). We use the statistical relation between mother presence and survival quantified by Parker et al. (2021) to construct a vector $\boldsymbol{\alpha}$ representing the age-specific proportional decrease in survival due to the absence of a mother (Supplementary table S1). Juvenile elephants up to two years old do not survive in the absence of their mother ($\boldsymbol{\alpha}(1:2) = 1$). The survival of juveniles between two and eight years old is reduced by 14.27 percent ($\boldsymbol{\alpha}(3:8) = 0.1427$). The survival of females between nine and eighteen years old decreases by 3.87 percent ($\boldsymbol{\alpha}(9:18) = 0.0387$) in the absence of their mother. The presence of the mother does not affect the survival of older females ($\boldsymbol{\alpha}(19:63) = 0$). The probability of a living mother for an individual of age x under a poaching pressure μ has been derives earlier

and is indicates with $\delta^{\mu}(x)$. With this quantity, the effect of the presence of a mother on survival is incorporated in the survival matrix:

$$\mathbf{U}^{\mu,\delta^{\mu}} = \mathbf{U}^{\mu} \text{ diag}\left(1 - \boldsymbol{\alpha}_i \left[\delta^0(i) - \delta^{\mu}(i)\right]\right) \qquad i = 1, \ldots, \omega \tag{13}$$

The entries in the baseline survival matrix ($\mathbf{U}$) are estimated while juvenile survival was affected by the presence of their mother. This is accounted for in equation (13) by considering the difference in expected presence of a mother with poaching ($\delta^{\mu}(x)$) and the expected presence of the mother without poaching ($\delta^0(x)$) instead of the absolute expected presence of the mother. As a result, the survival matrix without poaching calculated by equation (13) is equal to the survival matrix constructed from the estimated baseline survival probabilities ($\mathbf{U}^{0,\delta^0} = \mathbf{U}$).

The second effect of interactions among family members is an increase in fertility of young females due to the presence of a sister. We use the statistical relationship between the presence of a sister and the fertility of an individual, quantified by Lynch et al. (2019), to construct a vector $\boldsymbol{\beta}$ representing the age-specific fractional increase in fertility due to the presence of at least one sister (supplementary table S2). The values in this vector are calculated as the difference in the probability of successfully reproducing with and without at least one sister around, divided by the probability of successfully reproducing without a sister around.

The probability that an individual of age x under poaching pressure μ has at least one sister is given by equation (6) and is indicated with $\nu^{\mu}(x)$. With this quantity, the effect of the presence of at least one sister on fertility is incorporated in the fertility matrix:

$$\mathbf{F}^{\mu,\nu^{\mu}} = \mathbf{F}^{\mu} \text{ diag}\left(1 + \boldsymbol{\beta}_i \left[\nu^{\mu}(i) - \nu^0(i)\right]\right) \qquad i = 1, \ldots, \omega \tag{14}$$

Equation (14) uses the presence of a sister without poaching (ν_0) to correct for the effect of sisters on fertility when the baseline fertility was estimated. As a result, the fertility matrix without poaching calculated by equation (14) is equal to the fertility matrix constructed from the estimated baseline survival probabilities ($\mathbf{F}^{0,\nu^0} = \mathbf{F}$).

The third effect of family interactions is an increase in juvenile survival with an increase in the age of the oldest female in the family, which is usually the matriarch of the family (Foley

et al., 2008; Peron et al., 2019). This relationship was quantified to be 0.047 on a logit-scale for individuals up to 8 years old (Peron et al., 2019). The age of the oldest family member in the kinship network under poaching pressure μ is given in equation (9) and is denoted as $\gamma^{\mu}(x)$. With this relationship we can calculate a vector $\boldsymbol{\theta}$ with the age-specific proportional increase in survival due to the matriarch age.

$$\begin{aligned} \boldsymbol{\theta}^{\mu,\gamma^{\mu}}(i) &= \frac{1+\exp(0.047\gamma^{0}(i))}{1+\exp(0.047\gamma^{\mu}(i))}\exp(0.047\left(\gamma^{\mu}(i)-\gamma^{0}(i)\right)) \quad && i=1,\ldots,8 \\ \boldsymbol{\theta}^{\mu,\gamma^{\mu}}(i) &= 1 && i=9,\ldots,\omega \end{aligned} \tag{15}$$

Again, equation (15) uses the expected oldest age in the family without poaching (γ^{0}) to correct for the effect of the oldest age in the family on juvenile survival at the moment the baseline survival probabilities were quantified. As a result, the proportional increase of survival without poaching calculated by equation (16) is a vector of ones ($\boldsymbol{\theta}^{0,\gamma^{0}} = \mathbf{1}$). With this vector for the proportional increase in survival due to the matriarch age, we can calculate the survival matrix:

$$\mathbf{U}^{\mu,\gamma^{\mu}} = \mathbf{U}\ \mathrm{diag}\left(\boldsymbol{\theta}^{\mu,\gamma^{\mu}}\right) \tag{16}$$

Model results for African elephants

The model described in the modelling framework section provides a framework for investigating the population-level effect of poaching, and the ways in which family structure modifies those effects.

Population growth effects

Poaching reduces the growth rate of the elephant population (Fig. 2). In the absence of family feedback, the population will grow as long as the poaching pressure is below approximately 0.095, and will decrease if poaching pressure is above this value. The feedbacks between kinship structure and the individual life histories all amplify the effect of poaching on population growth. As a consequence, poaching has a stronger negative effect on the population growth when these

interactions are considered. Family feedback mechanisms reduce the critical poaching pressure above which the elephant population will decrease in size (Fig. 2).

Relatedness

As Focal ages, her average relatedness to her family group exhibits three distinct stages, which are mainly driven by the birth and death of kin in the maternal line of Focal (e.g. mothers, grandmothers, daughters and granddaughters) (Fig. 3). Initially, the average relatedness decreases with the age of Focal during the juvenile period. This pattern arises because some of the most closely related kin (e.g., mothers and grandmothers) of Focal might die, while Focal produces no new closely related kin in the form of daughters. The average relatedness to the kinship network begins to increase as soon as Focal starts to reproduce, because the daughters of Focal are always closely related to her. At old age, the average relatedness to the kinship network decreases again, because the death of Focal's daughters leaves only more distant relatives such as great-granddaughters and nieces.

An increase in poaching pressure increases the average relatedness to the kinship network and also amplifies the increase and decrease in relatedness throughout the life of Focal. These patterns emerge because poaching decreases the number of distantly related individuals such as aunts, cousins and nieces to a disproportionately large extent compared to kin in the maternal line of Focal such as mothers and daughters.

Figure 4 shows the relationship between poaching pressure and the average relatedness to the family group, as affected by the various family feedback effects.The expected relatedness increases with poaching pressure. The family feedbacks all increase the expected relatedness of Focal to her kinship network, because all these interactions amplify the effect of poaching.

Effect of mothers on juvenile survival

The presence of a mother increases the survival of juvenile individuals. Poaching strongly decreases the presence of the mother of Focal (Fig. 5). The feedback between the survival of Focal and the presence of her mother does not strongly affect the presence of the mother itself (Fig. 5) or other direct ancestors such as grandmothers and great-grandmothers. However, the additional feedback of mothers on juvenile survival substantially decreases the number of other kin such as daughters, granddaughters, sisters, aunts and nieces (Supplementary figure S2). Consequently, the feedback of mothers on the survival of juveniles amplifies the impact of poaching on the population growth rate (Fig. 2).

Effect of sisters on fertility

The fertility of individuals up to 20 years of age decreases if they have fewer than one sister around. At young age, the expected number of sisters, and thus the probability that Focal has at least one sister, increases with age, because Focal's mother produces new sisters. At older ages, the expected number of sisters, and thus the probability of having at least one sister, declines because older sisters die off and no new sisters are produced anymore (Fig. 6). Poaching strongly decreases the number of sisters of Focal and thus the probability that Focal has at least one sister. The feedback between family structure and the survival slightly decreases the probability that at least one sister is present a bit further, but also affects the expected number of other family members (Supplementary figure S3). As a result, the effect of the presence of a sister on fertility amplifies the effect of poaching on the population growth rate (Fig. 2).

Effect of matriarch age on juvenile survival

The survival of juveniles increases with the age of the matriarch. We assumed that the matriarch is the oldest female in the family. As Focal grows older, the expected age of the matriarch increases and converges to the age of Focal (Fig. 7). This pattern occurs because the analysis

focuses on the kin of Focal, and thus is conditioned on the survival of Focal. The older Focal is, the more likely it is that Focal herself is the oldest female in the kinship network and therefore the matriarch.

Poaching reduces the number and the life expectancy of kin, resulting in a decrease in the expected oldest age in the kinship network. Additionally, poaching increases the likelihood that Focal's mother is the matriarch of the family. Meanwhile, poaching also reduces the survival of Focal's mother, possibly causing an additional decrease in the expected oldest age in the kinship network during the first years of Focal's life (Fig. 7).

The age of the matriarch affects the survival of juveniles. Incorporating this feedback further reduces the number of older kin, such as older sisters and aunts, which causes the expected oldest age to drop further during Focal's life (Supplementary figure S4). Interestingly, the feedback also shifts the age distribution of Focal's mother at the birth of Focal towards older ages, which counteracts the effect of the low number of kin and slightly increases the expected oldest age in the family at the birth of Focal. Regardless of these small particular effects, the effect of the age of the matriarch on juvenile survival reduces population growth rate, as a function of poaching pressure, more than any of the other feedbacks (Fig. 2).

Discussion

Interactions between kin, such as cooperation, alloparenting, knowledge sharing and other forms of assistance, can affect the life history rates of individuals (e.g. Bengtsson, 1978; Hamilton and May, 1977; Kramer and Meunier, 2019; Waldman, 1988). Because the dynamics of a population reflect the life histories of individuals, we can intuitively understand that the structure of a family network could strongly affect the viability and dynamics of a population.

Meanwhile, the structure of a family network is also shaped by the life histories of the family members (Caswell, 2019), creating opportunities for feedback mechanisms between individual life histories, family structures, and population dynamics. These feedback mechanisms may

influence how the viability and dynamics of populations with strong family interactions will respond to anthropogenic influences.

Here we obtain a framework for modelling populations with strong kin interactions by combining the matrix model for a kinship network (Caswell, 2019) with a matrix population model (Caswell, 2001) based on the same life history. The kinship model utilizes the life history rates from the population model to describe the abundance and dynamics of kin through the life of a focal individual. Meanwhile, the life history rates in the population model depend on specific parts of the kinship network calculated with the kinship model. Due to the mutual dependence between the kinship model and the population model, the stable kinship network and stable population structure can be obtained as the solution to a nonlinear equation. Both the kinship network and the stable population structure are time-invariant and the age-specific kinship network is the same for all individuals. From the resulting structure, it is possible to derive quantities such as the long term population growth rate, which is a common measure for the viability of the population.

Our analysis is based on the time-invariant version of the matrix kinship model. That model has been extended to a time-varying version (Caswell and Song, 2021). However, calculating short-term dynamics with family interactions might require an individual-based model. During transient dynamics the kinship network would differ among individuals and would therefore have to be calculated separately for every individual (DeAngelis and Grimm, 2014). Such an individual-based approach would be computationally expensive and require more information about the exact family composition of all individuals than does the analysis we present here.

In addition, we note that our analysis is based on the one-sex version of the kinship model, as is appropriate for a matriarchically-organized species like the African elephant. However, multi-state and two-sex versions of the model (Caswell, 2020, 2022) make it possible to apply our modelling framework to species with a wide range of population structures and family interactions.

Our analysis of African elephants provides an example of how individual interactions can

affect population growth, in particular in response to poaching. The analysis is possible because of documented interactions among female African elephants: an increase in juvenile survival due to the presence of their mother (Parker et al., 2021), an increase in fertility of young females due to the presence of a sister (Lynch et al., 2019), and an increase in juvenile survival with the age of the oldest female in the family group (Foley et al., 2008; Peron et al., 2019). These positive interactions between family members amplify the negative effect of poaching on the population growth rate.

This amplification occurs because poaching damages the structure of the kinship network (an effect commonly observed in wild populations of elephants (Aleper and Moe, 2006; Barnes and Kapela, 1991; Foley, 2002; Mkuburo et al., 2020)). The disturbance of the kinship network diminishes the positive effects of interactions between family members, resulting in an decrease in the survival and fertility of individuals in the population. This reduction in survival and fertility adds to the the direct mortality from poaching and so amplifies the effects of poaching on the population growth. The effects of poaching on the population growth might therefore be more severe than expected from models that do not include interactions between family members.

The population growth rate of large populations is increased by positive social interactions between family members, while the population growth rate of small populations is decreased due to the lack of these positive interactions. This may result in an Allee effect (Stephens et al., 1999). It is challenging to quantify and model such family-Allee effects because the interactions act on the family level rather but then are expressed at the population level (see figure 1). Interactions between family members might show up throughout the entire kinship network. We show that, at least for elephants, positive interactions between family members are essential for the viability and conservation of populations with a strong family structure.

Genetic relatedness between individuals can play a crucial role in the conservation of wildlife populations (Hohenlohe et al., 2021). The matrix kinship model offers the opportunity to predict relatedness within family groups based on individual life history rates. As such, it could serve as a null model for studies about relatedness within populations. The pairwise relatedness between

individuals predicted by our model for African elephants is very similar to the average pairwise relatedness within observed family groups (Archie et al., 2006; Wittemyer et al., 2009).

Our analysis does not include the potentially important processes of fission and fusion of elephant family groups (Archie et al., 2011; Wittemyer et al., 2005). Fission and fusion might especially affect the oldest age and the relatedness between individuals. Although core family units of African elephants are strong and their social networks robust (Goldenberg et al., 2016), family groups might blend temporarily based on environmental conditions and group size (Wittemyer et al., 2005).

Large family groups tend to split based on the relatedness, with closely related individuals more likely to end up in the same group (Archie et al., 2011; Wittemyer et al., 2009). This processes is roughly captured by limiting the family network model to Focal's great-grandmother, Focal's grandmother, and the descendants of Focal's grandmother. The absence of more distantly related family members could reflect a split of the family network based on relatedness. On the other hand, our model does not capture the fusion of small family groups. Although more closely related family groups are more likely to fuse (Archie et al., 2011; Wittemyer et al., 2009), the relatedness between these individuals might still be relatively low. Incorporating fission and fusion of family groups into the matrix kinship model is an open research problem.

Accounting for the effects of family interactions on population growth of social species requires a level between that of the individual and that of the population. The matrix kinship model, which analyzes the family network with the same tools used for population projections, provides a first step in this direction.

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JCC conceived the initial concept of this study, analysed the model and wrote the original draft. Both JCC and HC contributed to the model formulation and contributed to the writing of all stages of the manuscript.

Data and Code Availability

This paper does not include new data. All MATLAB code needed to reproduce the results are included as supplementary material with this publication.

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Tables

Table 1: Subsidy term and initial age structure of every kin type from a focal individual (Focal) adapted from Caswell (2019). The dynamics of the age structure of every kin type is calculated with the general formula: $\mathbf{k}(x+1) = \mathbf{U}\mathbf{k}(x) + \boldsymbol{\beta}(x)$. Although not indicated in the expressions in this table, the entries in the survival matrix $\mathbf{U}$ and fertility matrix $\mathbf{F}$ might include poaching and might depend on the age structures of some of the kin types.

Symbol	Kin type	Initial distribution $\mathbf{k}(0)$	Subsidy $\boldsymbol{\beta}(x)$
$\mathbf{a}$	daughters	$\mathbf{0}$	$\mathbf{F}\boldsymbol{\phi}(x)$
$\mathbf{b}$	granddaughters	$\mathbf{0}$	$\mathbf{F}\mathbf{a}(x)$
$\mathbf{c}$	great-granddaughters	$\mathbf{0}$	$\mathbf{F}\mathbf{b}(x)$
$\mathbf{d}$	mothers	$\boldsymbol{\pi}$	$\mathbf{0}$
$\mathbf{g}$	grandmothers	$\sum_i \boldsymbol{\pi}_i \mathbf{d}(i)$	$\mathbf{0}$
$\mathbf{h}$	great-grandmothers	$\sum_i \boldsymbol{\pi}_i \mathbf{g}(i)$	$\mathbf{0}$
$\mathbf{m}$	older sisters	$\sum_i \boldsymbol{\pi}_i \mathbf{a}(i)$	$\begin{cases} \frac{1}{2}\left[\frac{\lVert\mathbf{F}\boldsymbol{\pi}\rVert}{1-\exp(-\lVert\mathbf{F}\boldsymbol{\pi}\rVert)} - 1\right] & \text{if } x = 0 \\ \mathbf{0} & \text{if } x > 0 \end{cases}$
$\mathbf{n}$	younger sisters	$\mathbf{0}$	$\begin{cases} \frac{1}{2}\left[\frac{\lVert\mathbf{F}\boldsymbol{\pi}\rVert}{1-\exp(-\lVert\mathbf{F}\boldsymbol{\pi}\rVert)} - 1\right] & \text{if } x = 0 \\ \mathbf{F}\mathbf{d}(x) & \text{if } x > 0 \end{cases}$
$\mathbf{p}$	nieces via older sisters	$\sum_i \boldsymbol{\pi}_i \mathbf{b}(i)$	$\mathbf{F}\mathbf{m}(x)$
$\mathbf{q}$	nieces via younger sisters	$\mathbf{0}$	$\mathbf{F}\mathbf{n}(x)$
$\mathbf{r}$	aunts older than mother	$\sum_i \boldsymbol{\pi}_i \mathbf{m}(i)$	$\mathbf{0}$
$\mathbf{s}$	aunts younger than mother	$\sum_i \boldsymbol{\pi}_i \mathbf{n}(i)$	$\mathbf{F}\mathbf{g}(x)$
$\mathbf{t}$	cousins via older aunts	$\sum_i \boldsymbol{\pi}_i \mathbf{p}(i)$	$\mathbf{F}\mathbf{r}(x)$
$\mathbf{v}$	cousins via younger aunts	$\sum_i \boldsymbol{\pi}_i \mathbf{q}(i)$	$\mathbf{F}\mathbf{s}(x)$

Table 2: Minimum and maximum expected relatedness between a Focal individual and the various kin types. The maximum expected relatedness assumes that sisters share the same father, while the minimum expected relatedness assumes that all sisters have different unrelated fathers.

Symbol	Kin type	maximum relatedness (ζ^k_{max})	minimum relatedness (ζ^k_{min})
a	daughters	0.5	0.5
b	granddaughters	0.25	0.25
c	great-granddaughters	0.125	0.125
d	mothers	0.5	0.5
g	grandmothers	0.25	0.25
h	great-grandmothers	0.125	0.125
m, **n**	sisters	0.5	0.25
p, **q**	nieces	0.25	0.125
r, **s**	aunts	0.25	0.125
t, **v**	cousins	0.125	0.0625

Figure legends

Figure 1: Graphic representation of the interactions between the individual life history, the kinship network and the population dynamics.

Figure 2: Growth rate of the population under increasing poaching pressure with various interactions between family members.

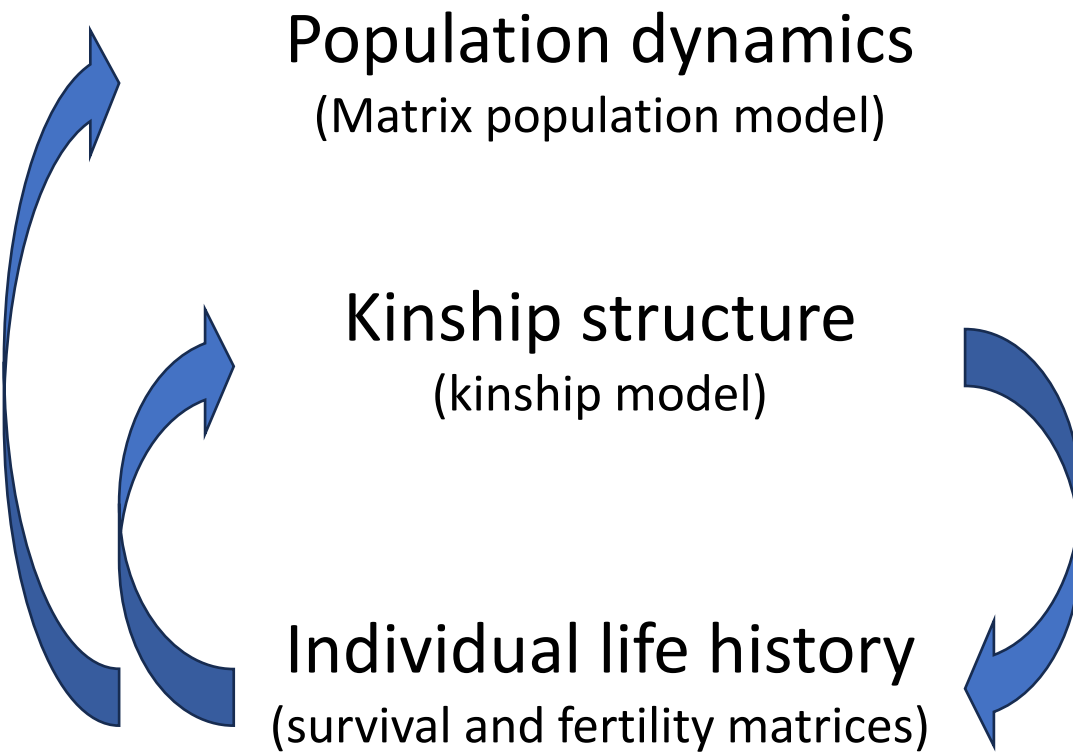
Figure 3: Average relatedness to the kinship network throughout the life of a Focal individual under three different poaching intensities. The lowest relatedness values are calculated with the assumption that all fathers are unrelated while the highest relatedness values are calculated with the assumption that all offspring of an individual have the same father.

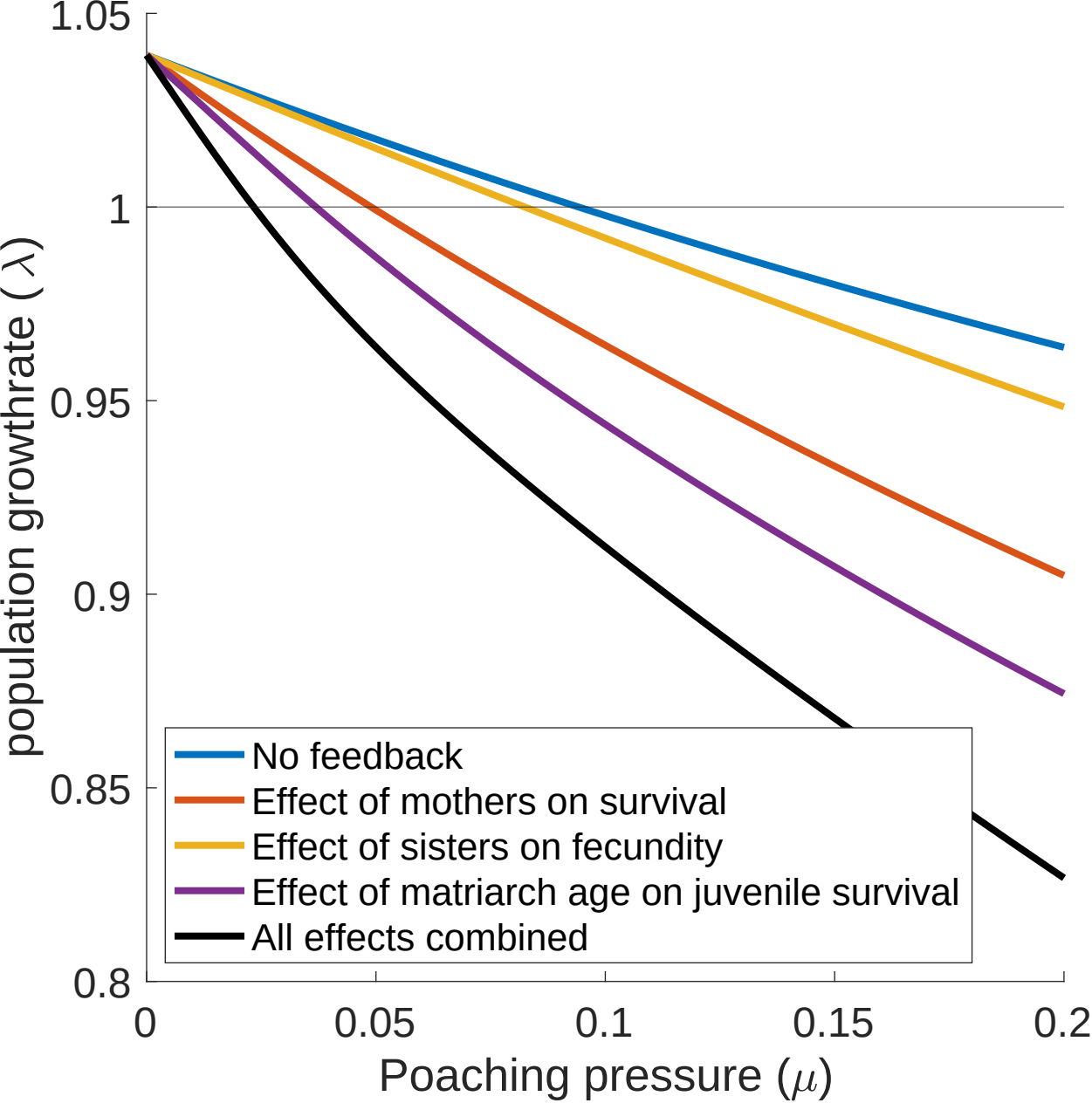
Figure 4: Expected relatedness of an individual in the population to the family group of that individual computed with various types of feedback mechanisms. Solid lines are calculated with a high relatedness in which sisters all have the same father and dashed lines are calculated with a low relatedness in which all fathers are completely unrelated.

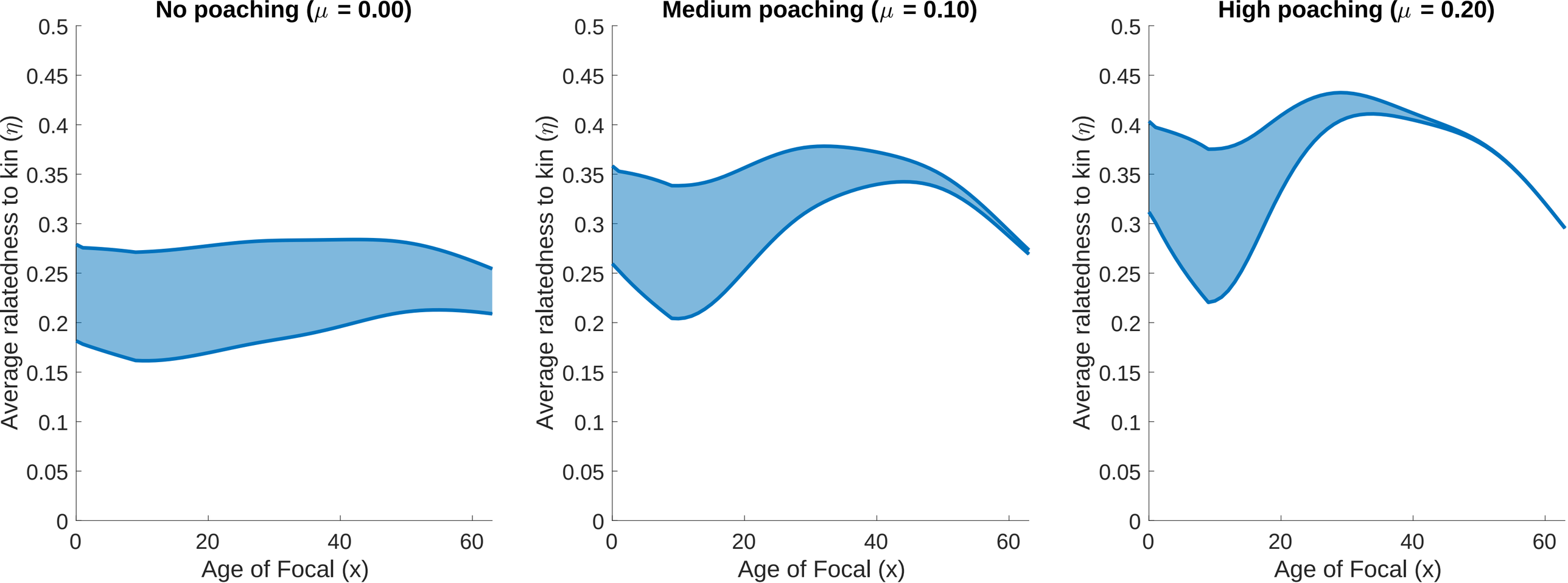
Figure 5: Expected presence of Focal's mother throughout her life, under various poaching pressures and with and without the feedback of mothers on the survival of juveniles. The dynamics of the extended kinship network throughout the life of Focal is shown in supplementary figure S2.

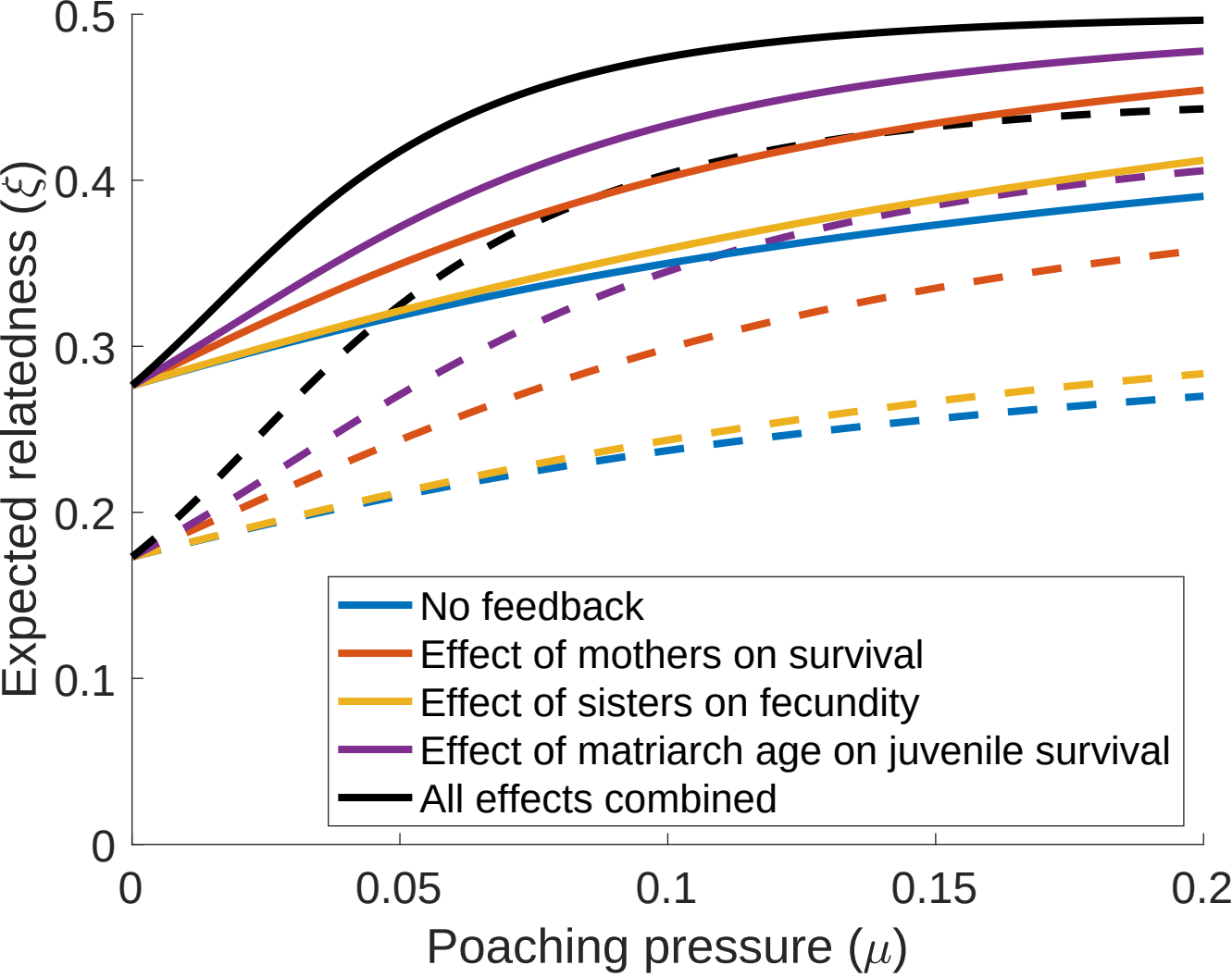
Figure 6: Probability of the presence of at least one sister as a function of the age of Focal, for various poaching pressures and with and without the feedback of sisters on fertility. The dynamics of the extended kinship network throughout the life of Focal is shown in supplementary figure S3.

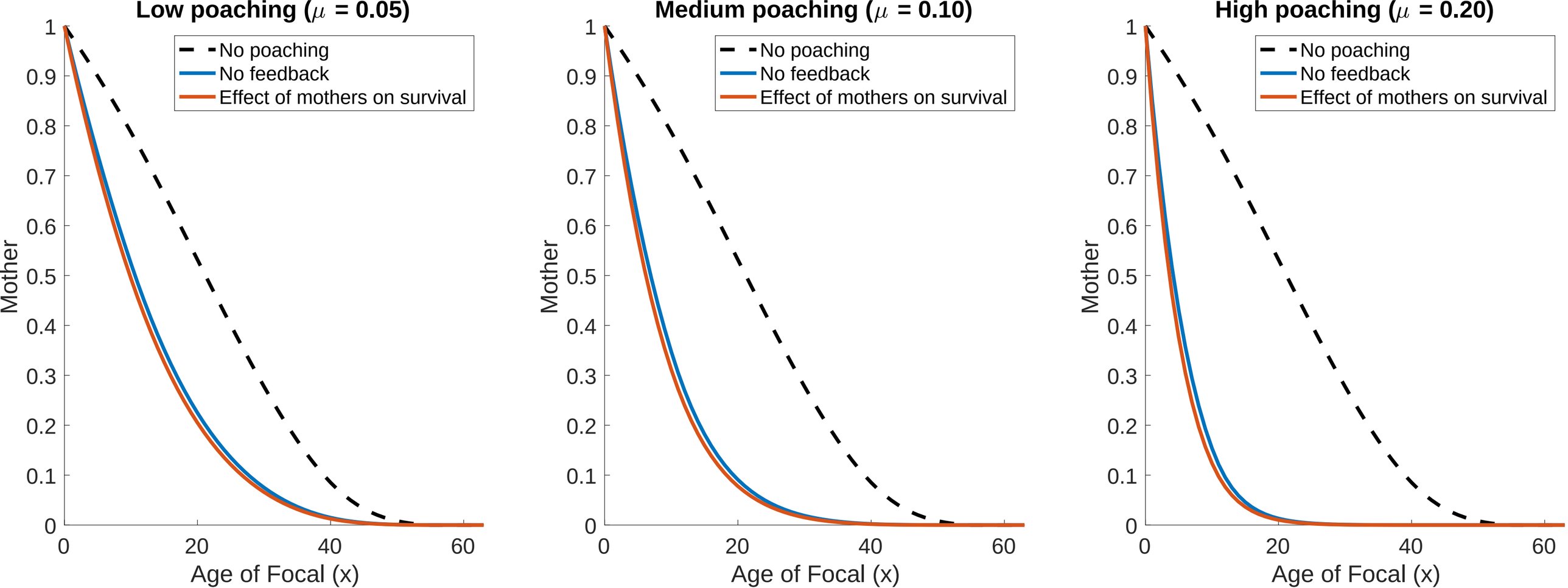
Figure 7: Expected oldest age in the kinship network, as a function of the age of Focal for various poaching pressures and with and without the feedback of mothers on the survival of juveniles. The complete kinship network throughout the life of Focal is shown in supplementary figure S4.

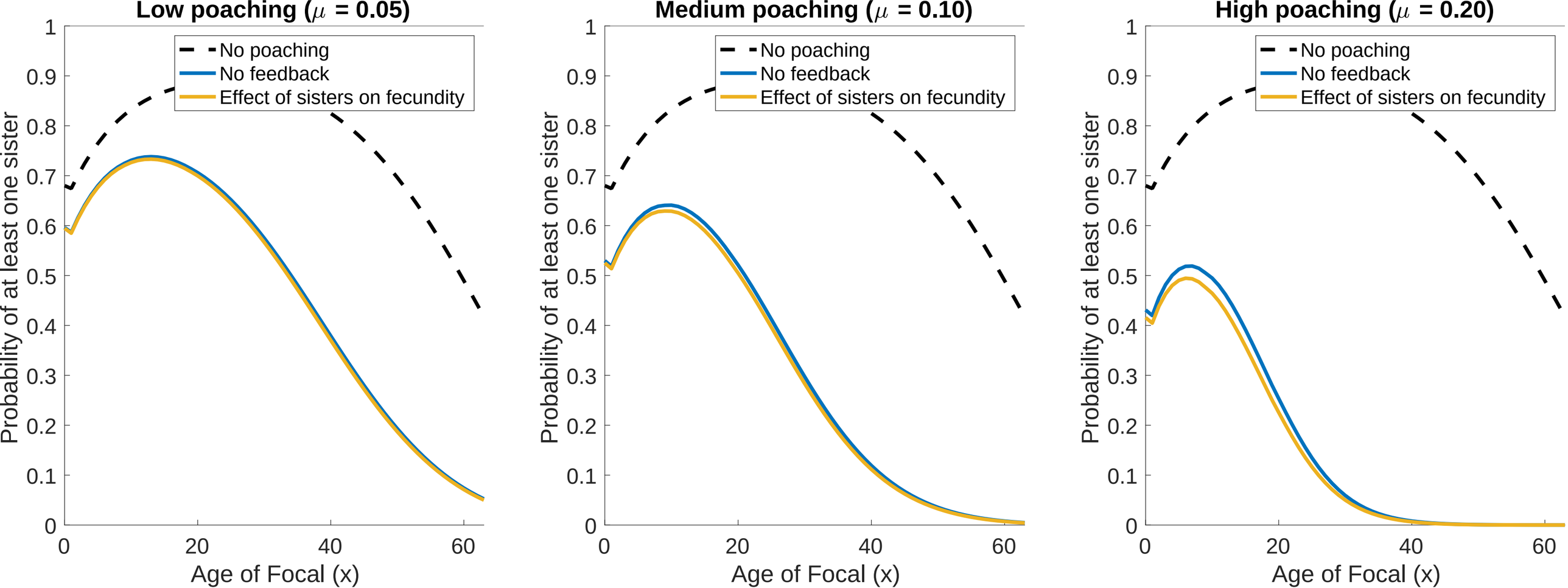

Population dynamics
(Matrix population model)
Kinship structure
(kinship model)
Individual life history
(survival and fertility matrices)

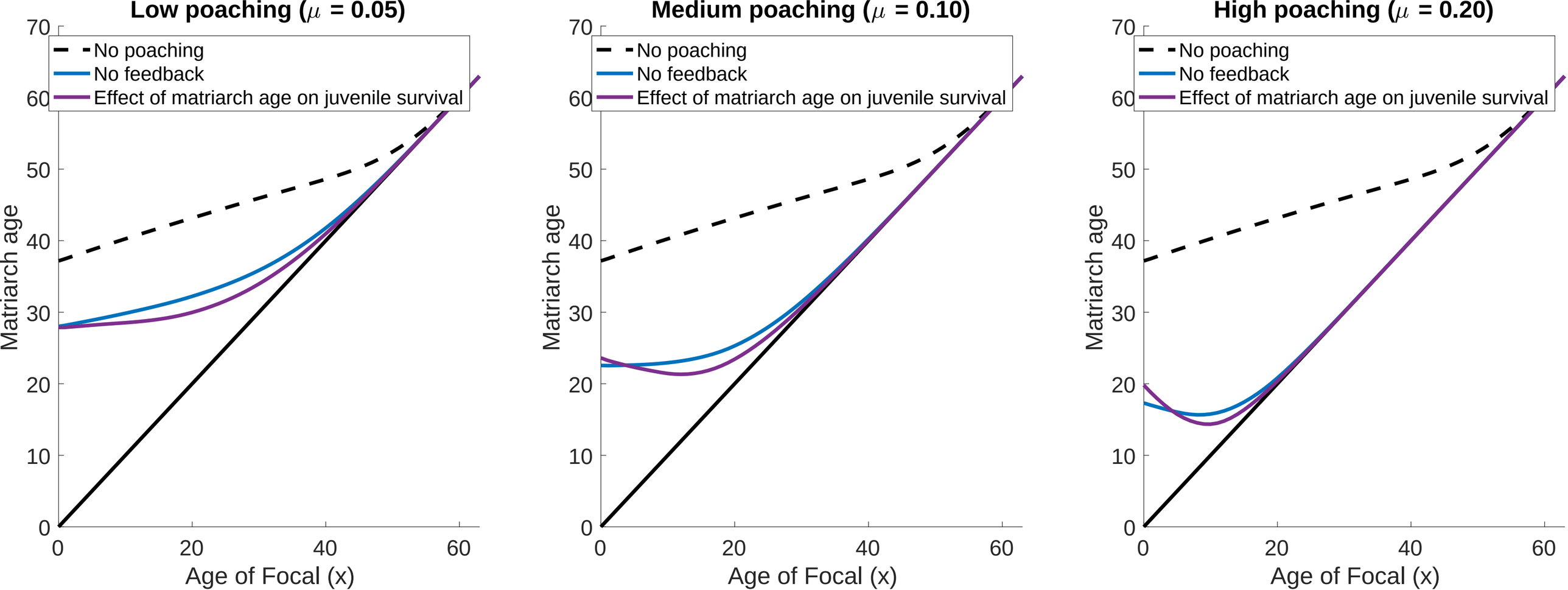

1.05
1
0.95
0.9
0.85
0.8
population growthrate (λ)
0
0.05
0.1
0.15
0.2
Poaching pressure (μ)
No feedback
Effect of mothers on survival
Effect of sisters on fecundity
Effect of matriarch age on juvenile survival
All effects combined


No poaching (μ = 0.00)
Medium poaching (μ = 0.10)
High poaching (μ = 0.20)
Average ralatedness to kin (η)
Age of Focal (x)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0
20
40
60


0.5
0.4
0.3
0.2
0.1
0
Expected relatedness (ξ)
0
0.05
0.1
0.15
0.2
Poaching pressure (μ)
No feedback
Effect of mothers on survival
Effect of sisters on fecundity
Effect of matriarch age on juvenile survival
All effects combined


Low poaching (μ = 0.05)
Medium poaching (μ = 0.10)
High poaching (μ = 0.20)
No poaching
No feedback
Effect of mothers on survival
Mother
Age of Focal (x)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
20
40
60


Low poaching (μ = 0.05)
Medium poaching (μ = 0.10)
High poaching (μ = 0.20)
No poaching
No feedback
Effect of sisters on fecundity
Probability of at least one sister
Age of Focal (x)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
20
40
60


Low poaching (μ = 0.05)
Medium poaching (μ = 0.10)
High poaching (μ = 0.20)
No poaching
No feedback
Effect of matriarch age on juvenile survival
Matriarch age
Age of Focal (x)
0
10
20
30
40
50
60
70
0
20
40
60